DEVELOPMENT OF MANAGEMENT MODELS AND ASSESSMENT METHODS FOR RED DEER ON THE OPEN HILL IN SCOTLAND

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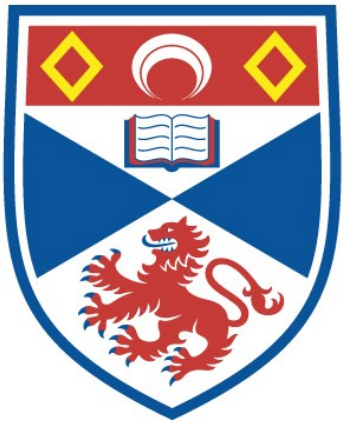
A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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submitted by Verena M. Trenkel

for the degree of PhD

April 1998

I, Verena M. Trenkel, hereby certify that this thesis, which is approximately 44,000 words in length has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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I was admitted as a research student in November 1993 and as a candidate for the degree of PhD in October 1997; the higher study for which this is a record was carried out in the University of St. Andrews between 1993 and 1997.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD in the University of St. Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Abstract

Models to assist the management of red deer on the open hill in Scotland and methods for estimating red deer abundance were studied in this thesis.

Currently red deer abundance is assessed by census methods with no estimate of precision. A coefficient of variation of 11-13% was estimated as the precision of repeated census counts on Rum. Misclassification in census counts was studied. Mean relative differences between two simultaneous independent counts were -0.9% (0.16) for stags, -0.5% (0.10) for hinds and 4.4% (0.61) for calves. Numbers in brackets are standard errors. Aerial line transect methodology for estimating deer numbers was tested. Mean estimates were comparable to a census count. In a case study comparison between line transects and census counts the former were shown to be quicker and cheaper for large areas.

Past numbers of red deer on the open hill in Scotland estimated by Markov chain Monte Carlo methods, suggested a 30% increase between 1970 and 1992, followed by a small decrease since. Convergence problems lead to reservations about the results.

A postal questionnaire survey provided information about current management practices and data availability. An age and sex structured stochastic population dynamics model for red deer was developed incorporating age, sex and density dependent survival rates and weight dependent fertility rates. An updating algorithm was proposed for calibrating the model parameters for any population using only count and cull information for that population. Prior parameter values were obtained from

well studied populations. The updating algorithm was based on approximate sequential Bayesian estimation carried out by simulation. Additional features were linear filtering of population estimates and a smoothed bootstrap to generate model parameter estimates. The linear filtering reduced one step ahead prediction errors. The smoothed bootstrap allowed substantial reduction in the number of simulations. For an example red deer population posterior parameter values produced smaller variances of predicted numbers compared to prior parameter values. The calibrated model was used to investigate the effects of alternative culling strategies for a red deer population.

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Chapter 1 Preface

The development of models to assist the management of wild red deer populations on the open hill in Scotland is the main theme of this thesis. The scope of this research extends to red deer on the open hill only. Traditionally red deer in forestry have been dealt with separately from those on the open hill. The former are part of the realm of the Forestry Commission whereas the latter are the responsibility of the Deer Commission for Scotland (formerly Red Deer Commission). This distinction is somewhat blurred in many areas, where increasing numbers of animals have access both to forest areas and the open hill. Recent efforts to rejuvenate and increase the areas of Caledonian pine forest, and ongoing expansion of forest plantations, have changed the open hill habitats. Hence, the management of open hill populations increasingly includes populations that have access to forest areas. On 77% of holdings surveyed in 1995, the open hill red deer populations had access to woodland or forestry plantations (Trenkel *et al.*, 1996). However, this thesis is targeted at open hill populations.

In chapter 2, the literature on wildlife management methods and approaches was reviewed. Some red deer populations in Scotland have been researched intensively and an overview of past ecological research on red deer was attempted. Many opinions have been put forward about red deer management practices and preferences in Scotland but little up to date information exists. A questionnaire survey was carried out to fill this gap. The results served as a basis for the subsequent development of management models.

In chapter 3, population abundance assessment methods were reviewed. Abundance

estimates were an integral part of wildlife management. They form the basis for modelling population dynamics. The precision of the currently used census method for counting red deer on the open hill was assessed. Aerial line transect methodology was evaluated as a feasible alternative method and compared to the census method in a cost-effort analysis.

In chapter 4, an estimate of the historic number of red deer on the open hill was attempted using Markov chain Monte Carlo methods.

In chapter 5, a stochastic population dynamics model for red deer was developed as part of a management model to assist deer managers. The management model makes it possible to explore the consequences of different culling strategies. A simulation based updating algorithm for calibrating the population dynamics model using local count and cull information was proposed. This updating algorithm was based on methodology which combines sequential Bayesian parameter estimation by simulation with linear filtering of population estimates. Simulation studies explored some of the aspects of the proposed updating algorithm. The updating algorithm was then used to calibrate the population dynamics model for two Scottish red deer populations. The effect of classification bias in census counts on calibrated parameter values was studied.

In chapter 6, the calibrated population dynamics model was used to illustrate how the management model might be used to explore alternative culling strategies for a red deer population. The implications of classification bias in counts for identifying culling strategies to keep the population stable were explored in a case study.

Chapter 7 draws together the conclusions on the work presented in this thesis and discusses future work.

Chapter 2 Overview of red deer management

2.1 Red deer on Scottish open hills

In the Scottish uplands, red deer were a common quarry of the Mesolithic hunters (Clutton-Brock and Albon, 1989) and have been hunted to varying degrees ever since. Originally a forest dweller, red deer have adapted to Scottish open moorland and retreated to high ground when forest availability diminished (Hart-Davies, 1978). Red deer numbers in Scotland rose and fell over the centuries, reflecting the current importance of other land uses such as sheep and timber production. Until the turn of the century no real attempts were made to estimate population sizes. Henry Evans (1890) was one of the first to attempt a count of red deer on the island of Jura on the Scottish west coast. The second world war saw a decrease in deer numbers, after which the Nature Conservancy was assigned the task of counting red deer in Scotland. In 1959 the Deer (Scotland) Act enacted the regulation of red deer hunting by introducing a closed shooting season and by setting up the Red Deer Commission which in future was to oversee all issues related to red deer in Scotland. Since then, the season for stag shooting runs from 1 July to 20 October. The hind season follows from the 21 October to 15 February. Outside this period, red deer can only be shot if found marauding on agricultural or forestry land or are causing damage to the natural heritage or endangering public safety. Since 1959 the Red Deer Commission has been responsible for collecting information on red deer numbers and the numbers of animals culled every year. In a recent amendment to the deer legislation (Deer (Scotland) Act 1996) the name of the Red Deer Commission was changed to the Deer Commission for Scotland reflecting the increased responsibilities and powers this act brought. Right from its early

days the Red Deer Commission not only carried out census counts of red deer but also provided advice on red deer management for interested land owners.

In Scotland, in contrast to other countries, the right to shoot belongs to the owner of the land on which the deer happen to be during the shooting season. Deer populations recognise no estate boundaries and any sensible management therefore should be coordinated across estates which 'share' the same distinct population. In order to do this Deer Management Groups have been set up comprising estates that host relatively discrete red deer population (RDC, 1986). However, although red deer are recognised as a common property resource (Howell, 1990), management of red deer so far has not been carried out according to those principles (Hanley and Sumner, 1995). In short, any cooperation between different land users relies on the voluntary principle which does not seem to have led to any agreements between the beneficiary of deer and those people having to suffer the impact of deer on their land.

2.2 Wildlife management methods

Natural resource management has a long history. Fish and wild mammal populations have been the subject of numerous studies, often concentrating on optimal exploitation strategies (e.g. Hilborn and Walters, 1992; Caughley and Sinclair, 1994). Man's desire to maximise the sustainable harvest of natural resources has been a driving factor in many cases. With increasing computer power in recent years, management advice has moved from general rules established under certain conditions to more 'online' methods based on population models. This historical development will be traced below in relation to the management of wild populations, with the emphasis on red deer.

2.2.1 Management based on rules

Experience and scientific research have led to the formulation of guidelines for red deer management. The Deer Commission for Scotland recommends that estates shoot a sixth of the red deer population annually in order to keep the population stable (pers. comm. C. McLean). Clutton-Brock (1991) derived rules regarding a desirable sex ratio in a managed herd from observations in the field. He stated that if a herd was managed to maximise meat production, a high number of hinds could be kept. As a consequence, stag numbers would go down as their survival would be depressed. Thus, a high hind-to-stag ratio would result. If however a herd was managed for trophy hunting for which mature stags are the main interest, female numbers should be low, allowing stags access to higher quality food. Buckland *et al.* (1996) confirmed these findings in a simulation study for a number of Scottish open hill populations. They found that if trophy hunting was the primary objective, the hind-to-stag ratio of animals older than one year could be kept below unity, thus having more stags than hinds.

Another method using the sex ratio to guide management is the so called linked sex harvest strategy (McCullough *et al.*, 1990). The linked sex harvest strategy has been devised mainly for populations where so far only male animals have been harvested. To apply this strategy, one would start to harvest female animals as well while keeping the effort for harvesting male animals the same as before. Gradually the female harvest would be increased until the male harvest starts to decline. When this happens the maximum yield of the population has been reached approximately. One advantage of the linked sex harvest strategy is that it does not require knowledge of population parameters such as survival and fertility rates. The method was evaluated for white-

tailed and mule deer with the result that it worked only for populations with certain population parameters (Lubow *et al.*, 1996). In order to decide whether the method would work or not it is necessary to know the survival and recruitment rates of a population, thus defeating the purpose of the method.

In a study of the red deer population in South Ross in the North of Scotland, Mutch *et al.* (1976) made detailed suggestions for the management of deer clans that form the South Ross population using a simple population dynamics model. A deer clan was defined rather loosely as a self-contained group of animals. Mutch *et al.* also provided a framework for red deer management based on simple indicators of performance and proposed a list of information that should be collected in order to monitor the population. Ageing of culled animals was one suggestion which is not routinely carried out in Scotland even 20 years after these recommendations were made.

2.2.2 Management using models

Population dynamics models have been a valuable tool for exploring a variety of questions regarding wildlife management. For example, Heppell *et al.* (1994) investigated the effects of various management actions intended to enhance red-cockaded woodpecker populations before any of them would be implemented in the field. Ways of reducing the total number of red deer without reducing the number of stalkable stags were explored by Buckland *et al.* (1996) with a deterministic population dynamics model. Other simple deterministic population dynamics model to assist red deer management have been developed by Scottish Natural Heritage and the Forestry Commission. Milner-Gulland (1994) studied different management strategies for the

saiga antelope using a deterministic population dynamics model. Petersson (1993) used a similar approach for reindeer harvesting. Thelen (1991) employed a population model to examine possible effects of different harvesting strategies on antler quality of elk. A somewhat different aspect of wildlife management was investigated by Walsh *et al.* (1995). They used a stochastic population dynamics model to assess expected effects of climatic change on a caribou population and were interested in the question of how much recruitment and survival rates would have to change before the caribou population would start to decline.

A number of researchers have concentrated on finding optimal exploitation strategies using population models. In particular, they were interested in finding the optimal yield or maximum sustainable yield for exploiting a population. A wealth of theories has been developed to underpin the results theoretically. The basis for these approaches is first an identifiable population model, second, knowledge of demographic parameters and third a set of restrictive conditions in order to obtain solutions. Beddington and Taylor (1973) looked at cropping patterns that would maximise yield of red deer populations given that only females were harvested. They found that it would be optimal to shoot out one age class completely and part of another one while maintaining a fixed total population size and a certain age structure. This work was extended by Beddington (1974) to include exploitation of males. The strategy crucially relies on being able to age animals in the field, wanting to keep the total population constant and knowing all demographic parameters. Beddington also pointed out the difference between an average optimal strategy over a number of years and an optimal strategy updated every year based on new information (latter is better). Clutton-Brock and Lonergan (1994) partly confirmed Beddington's results using an extended population model which

included sex-specific density related responses. They predicted that shooting all male animals aged five years or older and 16-20% of females aged one year or older would lead to the highest annual yields for the red deer population on the Isle of Rum on the West coast of Scotland. For populations where fecundity increases with age, Walters and Bandy (1972) suggested that periodic harvesting will lead to higher yield than harvesting every year.

A different route for finding optimal harvesting strategies has been dynamic and linear programming. Dynamic programming for deer management planning was explored by Davis (1967). Anderson (1975) looked at the effects different models have on optimal decisions, incorporating environmental variables in a stochastic serially correlated environment into the model. Stochastic dynamic programming for optimal exploitation and annual decision making based on the current observed state was proposed by Anderson (1985). However, he stressed the importance of a realistic model, which includes specification of the model and estimation of all its parameters. Before him, Stocker and Walters (1984) had explored optimal exploitation strategies for a hypothetical vegetation-deer system using stochastic dynamic programming.

Economics also has some views to offer on how best to exploit a population given economic factors. Objective functions for the cost of labour, the cost of land and income generated by red deer were used by Beddington (1975, 1974) to investigate economically optimal relationships between those quantities for different red deer population densities given a number of constraints. Multiobjective programming including economical and ecological goals to find optimal harvesting strategies has been applied to the exploitation of red deer and roe deer populations (Berbel and Zamora,

1995).

Johnson *et al.* (1997) suggested an adaptive management strategy for harvesting waterfowls in North America. Management regulations are considered every year combining current monitoring information, possible regulatory actions and their expected effects and uncertainty of population models. Every year the likelihood for each population model is updated by comparing its predictive performance based on last year's information with the information obtained from monitoring.

2.2.3 Decision Support Systems and Expert Systems

Decision support systems and expert systems are widely used tools for the practitioner in many fields of application. While expert systems are based on a number of rules and provide a definite answer to a given decision problem, decision support systems merely support the decision making process by making expert knowledge available. Decision support systems do not provide a definite solution to a problem. Hence, local experience is still required for decision making. White *et al.* (1985) suggested that the use of expert systems for wildlife management should be explored as they have been so successful in other areas. Decision support systems are used increasingly for population management (White *et al.*, 1987, Armstrong *et al.*, 1997a, 1997b; Donnely *et al.*, 1997; Freer *et al.*, 1997)

2.2.4 Ways forward for red deer management in Scotland

From the review of management methods above a number of common themes emerge which have not been dealt with extensively in the context of wildlife management. The starting point for many management methods is a population dynamics model which to a greater or lesser degree tries to encapsulate all processes judged to be important and about which enough is known to allow the formulation of relevant relationships. The next step is to find values for each of the parameters. In general one of two routes is taken. Either some realistic parameter values are assumed and the results treated as a theoretical exercise which might reveal some general principles (e.g. Beddington and Taylor, 1973; Stocker and Walters, 1984) or parameters are estimated for specific populations (e.g. Buckland *et al.*, 1996; Milner-Gulland, 1994) and the optimal management of those populations is sought. Decision support systems and expert systems take this one step further. Their basic principle is to combine results based on prior knowledge with local information provided by the user. In the case of red deer management following this route would mean developing a model that is applicable to any population of interest provided some local information is available. This local information would then be used to tailor the parameter values of the population dynamics model. If we had enough local information to estimate all model parameter values directly, there would be no need for such a system. However, for red deer populations on Scottish open hills this is rarely the case.

Another important consideration is the uncertainty in model parameter values and in the model specification itself. Some insight into the effects of different model specifications can be found in Stocker and Walters (1984), who model a

deer/vegetation system for different vegetation growth response functions. They found that optimal management depended crucially on the assumed functional type of the vegetation response. A commonly used strategy to investigate the effects of parameter values on management recommendations is to vary each parameter in turn by a fixed amount and observe whether and by how much the optimal management strategy would change. This method is called sensitivity analysis (e.g. Brown and Rothery, 1993).

Many of the more theoretical studies (e.g. Beddington 1974, Beddington and Taylor, 1973) have concentrated on finding optimal cropping strategies but in order to do this they had to introduce constraints and simple goals. In the Scottish highlands, red deer are only one of many, often competing, land uses and, as a consequence, management goals are rarely simple. This makes defining and finding "optimal" management strategies difficult. Furthermore, management can be looked at on different levels ranging from the national scale (chapter 4) to the population level (chapter 5). The appropriate level will depend on the context. In the next section the information available for input into a red deer management model will be assessed.

2.3 Information base for red deer management models

There are a number of sources providing information about red deer in Scotland. They can be divided into two broad categories: detailed population studies and census and cull data, available to a variable extent for the whole of the Highlands of Scotland. These two categories will be reviewed separately.

2.3.1 Population studies

Cameron (1923) published one of the earliest accounts of scientific observations of red deer in Scotland. He refers to work carried out by Henry Evans on the isle of Jura at the end of the 19th century. Evans collected a wealth of information about red deer; he counted them, recorded deaths and was interested in fertility and mortality rates. During the second half of the 20th century more and more scientists took an interest in red deer in Scotland. Since 1957 red deer have been studied intensively on the Isle of Rum off the Scottish west coast (e.g., Lowe, 1969; Clutton-Brock *et al.*, 1982; Clutton-Brock and Albon, 1989). A comprehensive review of the ecology of red deer in Scotland derived from studies of different populations was presented by Mitchell *et al.* (1977).

A multitude of studies consider the effects of environmental and population related factors on population dynamics. In two recent reviews Sæther (1997) and Putman *et al.* (1996) have summarised the literature on density-dependent and density-independent effects on red deer survival and fertility. In summary, there is evidence for negative effects of population density on calf winter survival (Guinness *et al.*, 1978) and some suggestions that adult survival is also affected (Mitchell and Crisp, 1981). For hinds and calves the number of hinds present rather than the total number of deer seems to be affecting survival (Clutton-Brock *et al.*, 1985). Fecundity was found to decrease with population density, whereas the difference in fecundity between milk and yeld hinds increases with population density (Clutton-Brock *et al.*, 1987).

Climate has been found to be the most important density-independent factor affecting

calf birth weights (Albon *et al.*, 1983; Albon *et al.*, 1987). Climate also affects summer calf mortality, adult winter survival (Clutton-Brock and Albon, 1982) and age at maturity for female animals (Langvatn *et al.*, 1996). The climatic impact is mediated through variation in vegetation growth and food availability and often affects body weight. Hind fertility is related to body weight (Mitchell, 1973; Mitchell and Brown, 1974; Albon *et al.*, 1983; Albon *et al.*, 1986).

Some detailed information is available on parameters affecting population performance of red deer in Scotland. Survival rates have been estimated for animals on Rum (Lowe, 1969), on the occasion of a severe winter in North-East Scotland (Mitchell, 1984) and for Glen Feshie, Glen Fiddich and Invermark (Mitchell *et al.*, 1973). Mitchell *et al.* (1986) provided estimates of fertility at age and natural mortality rates for the high density population at Glen Feshie. Similar details are available for the population at Glen Dye (Staines, 1978). Maximum longevity of red deer has been found to be about 20 years (Mitchell *et al.*, 1986).

2.3.2 Census and cull information

The Deer Commission for Scotland has been charged with the counting of red deer since 1959. They have split Scotland into 49 discrete counting blocks, each encompassing a more or less distinct population (Stewart, 1976). Each spring/late winter, four to five counting blocks are counted using a census method. The number of blocks counted depends on the size of the block and the weather. Snow drives animals down the hills into the valleys and makes them accessible to counters. In years of little snow, the counting programme is curtailed. Before the census information is

used for the management model (chapter 5), its precision will be critically evaluated and the potential suitability of other counting methods for the stated aim of red deer management will be assessed (chapter 3).

Landowners are required by law to report annually the number of deer (all species) shot on their land (Deer (Scotland) Act 1959). This information is then collated by the Deer Commission. On a more local level, Deer Management Groups and individual estates census deer populations using the same method as the Deer Commission. No central collection point for this information exists currently.

2.3.3 Current red deer management on Scottish open hills

There exists a vast literature on red deer biology and population dynamics of which only a small part has been reviewed. Little has been said about the strategies and goals of red deer management in the Scottish uplands. The main reason for this was that not much is known excluding anecdotal evidence. The most comprehensive study to date was carried out by Callander and MacKenzie (1991) who collated the available information on culls and counts and gave the legislative as well as political background. In order to assess current management practices on the open hill, local data collection and other issues related to red deer management, a postal questionnaire survey was carried out in cooperation with the Macaulay Land Use Research Institute. The results of this survey were used to guide the development of the red deer management model (chapters 5 and 6).

Survey design

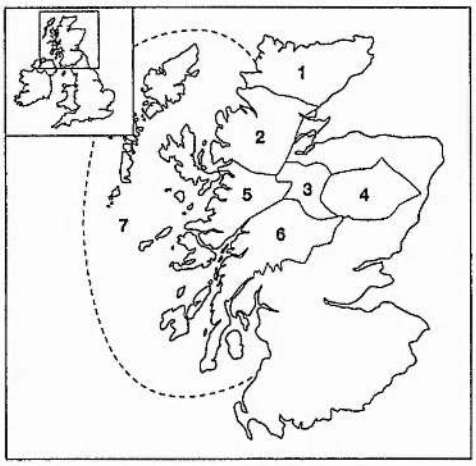
The survey attempted a census of all estates and farms (referred to here as 'holdings') that are required, under current legislation, to make annual returns to the Deer Commission for Scotland detailing the number of red deer culled. Owners of commercial forestry with no open hill land were excluded. In spring of 1995 a postal questionnaire was distributed to 515 different addresses, some of which received more than one questionnaire to cover different parts of a holding that might be managed differently.

The questionnaire was sent to all relevant holdings, so most of the uncertainty in the summary of returns is due to non-response. Replies were grouped by region and by the area of land accessible to red deer. Chi-squared tests were used to determine the probability that patterns at least as extreme as those observed occurred by chance under null hypotheses of identical underlying patterns of responses. These tests allowed assessment of the evidence for genuine differences in response patterns. They were not intended to determine what the total response would have been had all holdings replied to all questions. Respondents that did not answer a particular question were excluded from the calculations for that question only.

Responses

Of the 615 questionnaires distributed, 262 questionnaires were returned initially and a further 96 questionnaires were returned after a reminder letter was sent. Of the 358 returns, 322 came from the 467 holdings that had received or returned only one

questionnaire, which corresponds to a return rate of 69%. For holdings that had been sent more than one questionnaire and either returned more than one or none the number of returns that would have corresponded to the entire holding could not be determined. As a consequence, no response rate was calculated for these holdings.



	Region	No. responses
1	north	39
2	central north	55
3	central	42
4	east	49
5	central west	40
6	south	79
7	Western Isles	30
	unallocated	24
total		358

Figure 2.1. Map of Scotland showing the regions used to classify responses and table indicating the number of responses.

The holdings were grouped in two ways for the analysis. Firstly, they were classified into seven geographical regions based on the location of the holding (Figure 2.1). Secondly, the responses were classified according to the size of the area accessible to red deer on the holding. Four size categories were defined, with the intention that roughly equal numbers of holdings should fall into each category. The area classes selected were: holdings up to 17 km^2 (86 responses), those between 17 and 39 km^2 (84 responses), between 39 and 79 km^2 (84 responses) and holdings with more than 79 km^2 accessible to red deer (85 responses). Nineteen respondents did not give the area accessible to red deer.

Information collection by holdings

The majority (77%) of holdings reported that red deer regularly moved onto and off the holdings, probably on a seasonal basis. This not only affects the numbers of animals available to the holding for shooting but also affects the scale at which red deer should be managed. It also means that a management model for red deer (chapter 5) should be applied at the Deer Management Group rather than at the level of the individual holding.

Census counting of red deer is carried out by the Deer Commission for Scotland in various parts of Scotland each year. On 27% of holdings that responded the Deer Commission for Scotland made a count at some point between 1991 and 1995. In the same period, an additional 32% of holdings made a count themselves or in coordination with the relevant Deer Management Group but without the involvement of the Deer Commission for Scotland. Therefore, there had been at least one count on 59% of holdings between 1991 and 1995. For most holdings (89%) that do their own counts, the most recent count at the time of the survey was generally within the last one or two years. Based on the most recent count available, red deer densities on each holding were calculated (Figure 2.2). Average deer densities per region ranged from 7 to 14 deer per km^2.

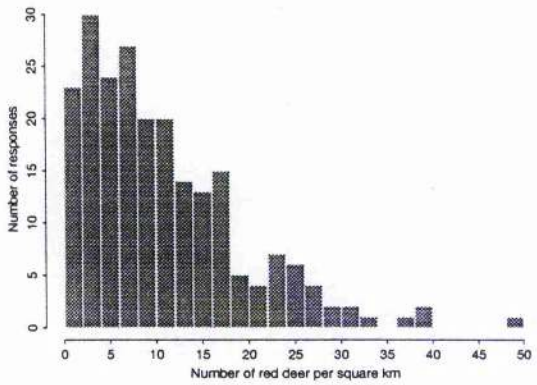


Figure 2.2. Deer densities on holdings based on the most recent census at the time of the survey.

More information relevant to the management of a population can be obtained from culled animals. Most holdings record the date, location and body weight of hinds and stags that have been shot (Table 2.1). Ageing culled animals is a necessary prerequisite for reconstructing the past population size and structure and estimating its current age structure, which is important for culling strategy decisions. Less than half the holdings note the age of an animal based on tooth wear for stags and even fewer do so for hinds.

Table 2.1. Percentage of holdings that record information from culled animals.

Type	Hinds	Stags
Date	78	84
Location	69	75
Weight	73	78
Age	38	49
Body condition	30	34
Status (yeld or milk)	39	-
Reproductive condition	28	-
Antler quality	-	47

Holdings can control the number, age group (young, mature or old) and sex of deer shot as part of the regular cull during the shooting season. Some culling strategies are more suited than others to reach certain management goals. Therefore, it is important to choose a culling strategy suitable for the desired goal. For example, by selectively shooting certain age groups, holdings can determine the future size and structure of the population.

In-season shooting of stags was carried out by 88% of holdings at some point during the previous three years. There is a regional pattern to this ($p=0.007$) with only 78% of holdings in the South (region 6) having shot stags and more than 90% in regions 2, 3, 4, 5 and 7 (Figure 2.1). The proportion of holdings that have carried out in-season stalking of stags increases with the size of the holding ($p=0.0008$). In-season hind culls were carried out by 85% of holdings during the previous three years with no difference between regions. A higher percentage of larger holdings carried out hind culls ($p=0.0001$).

Holdings vary in the current management policy used for determining the number of stags and hinds to shoot. In the case of in-season stag stalking, about equal numbers of respondents shoot a fixed number of stags, a fixed proportion of the stags, or do not have a single policy (Table 2.3). The most common policy for culling hinds was to shoot a fixed proportion of the hind population whilst only about half as many respondents shoot a fixed number of hinds. Time availability determines the hind cull for 13% of respondents, which is far more than for stags (7%).

Table 2.3. Management policies determining the size of the stag and hind cull on holdings (percentage). na = not asked

Management policy	Stags	Hinds
Fixed number	32	26
Fixed proportion	30	46
Fixed time available	7	13
Demand for stalking	2	na
No single strategy	29	na
Other strategy	na	15

The respondents were asked to rank the factors influencing hind cull levels. Controlling hind numbers on the holding was given as the major determinant factor for the number of hinds shot by 47% of holdings. Control of hind numbers in the wider Deer Management Group area was a determinant factor for only 18% of holdings. Venison production was stated to be the main determinant of the size of the hind cull on few holdings (7%).

Most holdings have no influence on the numbers, age or sex of deer shot as marauders. In both northern regions (regions 1 and 2), the east (region 4) and the Western Isles (region 7) of Scotland, over 44% of holdings have had marauding stags shot on their land during the past three years. For the remaining regions, this figure is between 30 and 40%. Marauding hinds have been shot on the land of over 40% of holdings in the central north, east and the Western Isles (regions 2, 4 and 7) compared to only 18% in the north (region 1).

During the shooting season, stag shooting can be let to clients or be carried out by the

owners and their staff. The motives and thus the age classes shot by the two groups of deer stalkers might be expected to be different, as clients could be more interested in shooting mature stags with impressive heads rather than those that would be best to control red deer numbers. The respondents were asked to rank the three age groups, immature (<6 years), mature (6-10 years) and old stags (>10 years) according to the degree to which they were targeted by clients. Rank 1 means that this age group is the most targeted, rank 2 that it is less and rank 3 means that it is least targeted. The same question was asked regarding the stags shot by the owner or holding staff. The main age group targeted both by guests/clients and owner/staff is mature stags (Figure 2.3). Old stags are also preferentially targeted on many estates, especially by the owner/staff. There was no significant difference between the targets of the two groups of stalkers, guests/clients and owner/staff ($p=0.57$). This indicates that the two groups of stalkers follow a similar strategy of targeting mature stags.

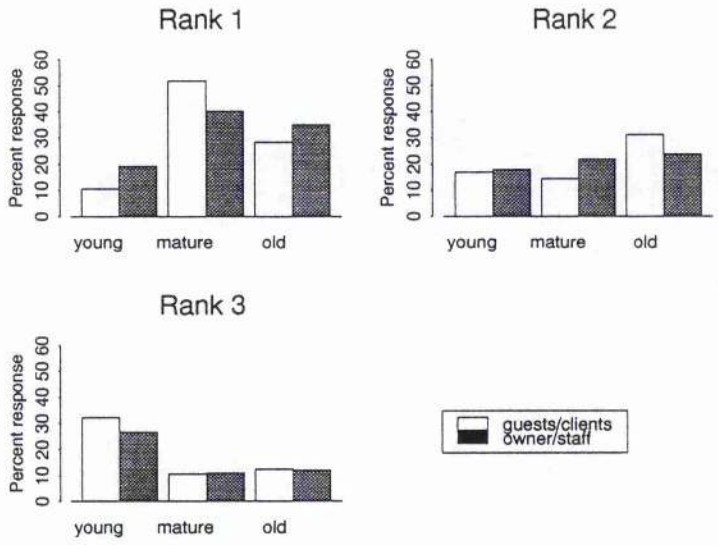


Figure 2.3. Age classes of stags targeted for stalking by two different groups of stalkers. Respondents were asked to give ranks to indicate the categories which were most (rank 1) to least (rank 3) targeted during the stag cull.

The targeting of hinds during the hind cull was also looked at. Five target groups were

offered: yearling hinds, yeld hinds (no calf at foot), old hinds, hind and calf pairs and unselective shooting. Again the respondents ranked these options according to the actual management practice on the holding. Old hinds are primarily targeted on most holdings; yeld hinds and hind and calf pairs also tended to be targeted (Figure 2.4). This targeting policy for hinds appears to be aimed at improving the health of individuals in the current population rather than shaping the future size of the population. It seems to contradict the stated goal for a majority of holdings to control hind numbers.

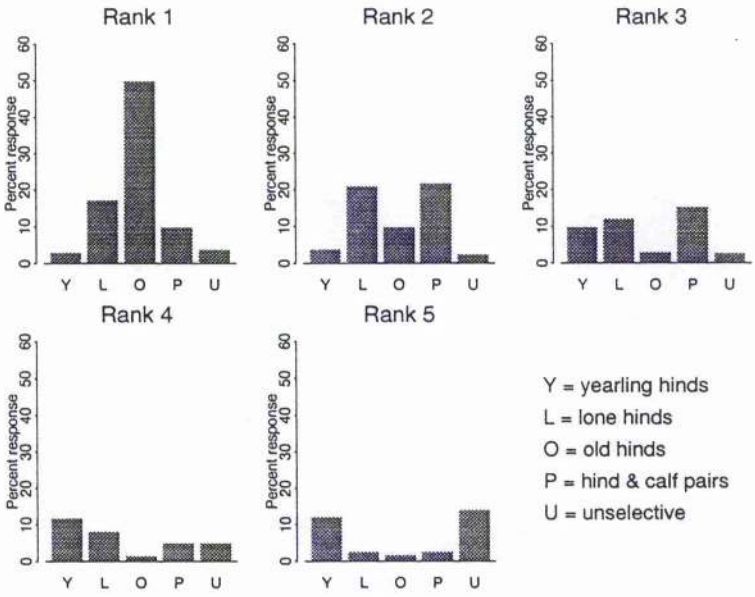


Figure 2.4. Categories of hinds targeted during the hind cull. Respondents were asked to give ranks to indicate the categories which were most (rank 1) to least (rank 5) targeted.

Red deer management provides income through venison sales and fees from sportsmen. The question about income from these two sources was phrased in relative terms, avoiding the contentious issue of money. Income from venison was more important than income from stalking on 39% of holdings, whereas income from lets was higher on 21% of holdings. On 27% of holdings lets and venison contributed equally to income. The holdings that did not respond to this question included all those holdings

that did not have any income from either lets or venison. The overall picture from this survey is that the contributions from venison and letting fees to holding income were about in balance at the time of the survey.

Stags were stalked by guests or paying clients during the previous three years on 74% of all holdings with little difference between regions. A holding size effect ($p=0.007$) was found with more larger holdings having stags stalked by guests or paying clients. The size of the holding was unrelated to the letting of hind shooting ($p=0.003$) with more than 50% of larger holdings having let hind shooting during the previous three years. The corresponding figure for holdings with less than 18 km^2 accessible to red deer was 24%.

Requirements for red deer management model

More than three quarters of holdings reported that red deer are moving on and off the ground during the year. This means that a management model for red deer should apply to areas larger than the holding, for example the Deer Management Group if it comprises a distinct population. It was found that a number of holdings do their own census counting. Hence this information might be assumed to exist at a local level. Only about half the holdings age culled animals. For many populations it will therefore be impossible to build up a picture of the age distribution directly and some way of handling this lack of information is required. A number of different management strategies were reported. Age selective culling was carried out on most holdings. This means that a management model needs to be age structured. Milk and yeld hinds were targeted differentially by many holdings and therefore should be modelled separately.

Chapter 3 Survey methods for estimating red deer abundance

3.1 Introduction

A variety of methods are available for obtaining estimates of population size (e.g. Mitchell *et al.*, 1977; Seber, 1986; Staines and Ratcliffe, 1987; Roseberry and Woolf, 1991; Buckland, 1992). The appropriate method depends on the species assessed and the type of habitat it is living in. For red deer in Scotland, open hill and forest plantations are the two most common habitat types. For management purposes, these have been considered to host separate populations. However, an increasing number of red deer populations primarily live on the open hill but also have access to forest plantations.

A number of different methods have been used to assess red deer population sizes both on the open hill and in forested areas in Scotland. The census method is the most commonly applied method on the open hill and is currently used by the Deer Commission for Scotland (Stewart, 1976). There are several problems with census methods. Firstly, animals staying in forest or other cover will tend to be missed by the counters. This leads to an undercount. Secondly, concern has been raised regarding the accuracy of census counts of red deer carried out by the Deer Commission for Scotland (Clutton-Brock and Albon, 1991). Thirdly, they are labour intensive as every animal has to be counted. As a result, most red deer populations have been counted only once or twice by the DCS during the last three decades.

Accuracy and precision of abundance estimates are the two main concerns when

comparing counting methods. If a counting method also classifies animals into different groups, the probability of misclassifying an animal and the conditions on which this might depend are also of interest.

In this chapter current knowledge and experience concerning the census method and alternative counting methods are summarised and evidence regarding the usefulness of these methods is evaluated. Estimates of classification error rates and accuracy of census counts were attempted. In a pilot study the aerial line transect method was used to estimate red deer numbers and the results were compared with those of a census count. A cost benefit analysis was carried out to compare the census method with the aerial line transect method. Finally, the effects of abundance estimation error when abundance estimates are used for management purposes was investigated in a simulation study.

3.1.1 Currently used counting methods

The census method is the current method of choice for assessing red deer abundance on the open hill in Scotland. Census methods rely on counting every individual animal and can be carried out on foot, by car or from a helicopter. They are not useful in densely forested areas, which limits their range of application in the Scottish Highlands as the areas covered by forest are slowly increasing and deer are gaining greater access to them.

Census methods do not provide an estimate of precision. However, one way of assessing the precision of census counts is to compare repeated counts of the same

population. Lowe (1969) compared counts of red deer on Rum carried out on two different days by the (then) Red Deer Commission and Nature Conservancy staff. Six (+ 0.6%) more animals were counted the second time in addition to the 1088 counted the first time. Lowe also reported on a study where on two occasions three counters counted the same animal groups. On the second date, 4.4% more animals were counted in total.

Youngson (1991) compared census counts of stags on Rum with estimates of population size based on population reconstruction and found most differences to be less than 13%. In an earlier comparison of counted and reconstructed numbers on Rum discrepancies ranging from -2.6 to -12.1% for stags, from 14.5 to 25.8% for hinds and from -30 to +10% for calves were found (Lowe, 1971). Clutton-Brock and Albon (1989, 1991) have carried out further comparisons. Caughley and Goddard (1972) proposed a method for improving estimates from inaccurate census counts based on an assumed relationship between mean and variance obtained from multiple counts. So far their method has not been used in Scotland.

Although misclassification seems to be recognised as an important problem, it has rarely been investigated systematically and with satisfying sample sizes. Some of the studies reported above, have also considered this problem as a side aspect of their investigations. In a review of counting methods for red deer Buckland (1992) recommended that a study should be carried out which would attempt to quantify the misclassification rate in the Deer Commission's census counts. Buckland also recommended that alternative methods should be tried out for red deer on the open hill. These recommendations are discussed in sections 3.2.2 and 3.3 respectively.

3.1.2 Alternative methods for open hill populations

There are a number of alternatives to the currently used census method. Line transect methodology has been used to estimate the abundance of many terrestrial mammals. The method allows estimation of the size of a population; it also gives an estimate of the precision of that estimate. Recent examples of line transect studies include the following. Whiptail wallaby numbers in heavily forested habitat were assessed by Southwell *et al.* (1996). Mugangu *et al.* (1995) estimated the density of the African buffalo in five different habitats, ranging from mudflats and steppes to woodland savanna. Population densities of large mammals like sambar, Asian elephant and gaur dwelling in deciduous forests were estimated by Varman and Sukumar (1995). Pojar *et al.* (1995) used aerial line transect methods in a sagebush steppe to assess pronghorn numbers. Several studies have used line transect methods to estimate ape numbers, and Plumptre and Reynolds (1996) address how best to do this. Several researchers have used line transect methods on deer populations. Gaillard *et al.* (1993) assessed the performance of line transect methods on a roe deer population of known size. Pinder (1996) estimated the density of marsh deer in a region of Brazil by line transect, strip transect and mark-recapture methods. White *et al.* (1989) estimated mule deer numbers in Colorado from aerial line transect surveys using a helicopter and Gill *et al.* (1997) estimated deer numbers in forests employing thermal imaging equipment to aid detection. There is a body of information about successful use of line transect methods under different circumstances and for different species.

Line transect methods seem to be promising for estimating red deer numbers on the Scottish open hill. The ability to detect all animals on the transect line and before they

can react to the survey is essential for the successful application of the method. As large areas have to be surveyed in Scotland, it would be useful to base any trial on an aerial platform, such as a helicopter or a fixed-wing aircraft. A feasibility study using aerial line transects from a helicopter for estimating red deer abundance has been carried out and is reported in section 3.3.

Other counting methods have been used for assessing various species around the world. The change-in-ratio method (e.g. Roseberry and Woolf, 1991) relies on assessing the ratio of two groups, e.g sex ratio on at least two different occasions when in the intervening time this ratio has been changed through some controlled measure, for example through culling of male animals only. It also relies on constant detection rates of both groups across sampling occasions. A number of theoretical studies have looked at estimators for the change-in-ratio method under different conditions and considered how to incorporate additional information (e.g. Udevitz and Pollock, 1995). Conner *et al.* (1986) assessed the sample size required to achieve a specified precision in the estimate of deer numbers with the change-in-ratio method. The change-in-ratio method seems to be a suitable candidate for assessing red deer on the open hill in Scotland and it would probably also be able to cope with situations when parts of the population are hiding in forestry during the assessment period, provided the ratio of the two groups is the same in and outside the forest. One drawback of the method is that it relies on assessing the same population twice. Furthermore, one also has to be able to change the ratio of the two groups substantially and in a known way. This problem could be overcome, as the stag stalking season in Scotland takes place before the hind cull and the number of animals culled is known. Thus the population assessment would take place before and after the stag culling season. The periods before and after the hind cull

are less suitable, as the hind cull stops mid February when animals are dying naturally which makes it difficult to account for the number of animals that have been removed from the population. The requirement of constant detectability might be a problem due to the sex segregation of red deer during the year and their aggregation for the rut which would coincide with the second assessment in autumn. Roseberry and Woolf (1991) found that variability in detection of different groups of white-tailed deer made the change-in-ratio method unreliable.

Mark-recapture methods are widely used assessment methods for studying populations (e.g. Montgomery, 1987). They are based on marking part of the population on one or more occasions and resampling it once or more. There are several estimators for the total population size based on different assumptions. The Lincoln index for closed populations equates the proportion of marked animals in the sample to the proportion of marked animals in the population to estimate total population size. Bartmann *et al.* (1987) evaluated an aerial mark-recapture method for mule deer in woodland and compared the precision of density estimates obtained with different estimators. They concluded that different estimators provided comparable precision given that a large proportion of a small study population had been marked. Bowden and Kufeld (1995) developed a new procedure for constructing confidence intervals and used it for a Colorado moose population. As for the change-in-ratio method, the mark-recapture method requires two or more contacts with the population whose density is estimated. Furthermore, for obtaining total estimates of reasonable precision, it requires marking a large proportion of the population which implies substantial effort. Hence mark-recapture methods are probably not the first choice when assessing alternative counting methods.

The dung count method is particularly useful for assessing red deer numbers in forest and has been used in this context. The method relates the occurrence of dung to the number of animals present. Fuller (1991) compared dung count density estimates for white-tailed deer with population estimates derived from aerial surveys and concluded that the estimates from the two methods did not agree at all which seems to be limiting the use of the dung count method. In Scottish forests, using the accumulation of faeces to estimate red deer densities has been tested by Mitchell and McCowan (1979). They encountered problems due to varying decomposition rates of faeces which made it difficult to relate accumulation of faeces to deer densities. The Forestry Commission (Ratcliffe, 1987) recommends dung counts for estimating red deer densities in forests as they are one of the few feasible methods currently available. However, for the open hill some of the methods discussed above seem to be easier to apply, therefore it does not seem advantageous to resort to dung counts which might only lead to relative estimates of abundance.

3.2 Assessing the census method

3.2.1 Precision of census method: Comparing repeat counts on Rum

The precision of counts obtained with the census method has rarely been evaluated. An estimate of this precision has been attempted based on repeated counts carried out on Rum. Over many years the red deer population on Rum has been studied intensively (Clutton-Brock *et al.*, 1982; Clutton-Brock and Albon, 1989). In the context of this ongoing study the population in the North Block of Rum has been counted repeatedly by F. Guinness and others. Counts made between 1978 and 1991 were available for

analysis. Over the same period the Deer Commission for Scotland has been counting red deer on the whole island annually. These parallel data sets have been used to assess precision in census data.

The DCS counts for the North Block have been extracted from maps of the island with the counts marked upon by superimposing the boundaries of the North Block. This procedure might have led to slight inaccuracies in some cases. F. Guinness et al. have counted the North Block several times every year. Two sets of counts within five days on either side of the DCS counts were selected. The counts made before the DCS's are referred to as "B" and the counts made after the DCS counts as "A". Ten counts were available for the comparison "B"-DCS, eleven for "A"-DCS and ten comparisons were made between non-DCS counts ("B"-"A").

Before an estimate of precision for census counts can be obtained from this data set, it has to be ensured that there is no significant difference between the DCS and non-DCS counts. A number of analyses were carried out to ensure this condition was satisfied. On average, the DCS counts for stags were higher than both other counts (Table 3.1). For hinds, the DCS count lay between the other two counts on average. The greatest difference between DCS and non-DCS counts was found for calves and the total number of deer.

Table 3.1. Mean difference (s.e) between counts in North Block of Rum (1978-91). "B" are counts made before and "A" after the DCS counts by F. Guiness et al.

	Count source		
	"B"-DCS	"A"-DCS	"B"- "A"
STAGS	-3.4 (3.8)	-6.5 (3.6)	1.8 (5.5)
HINDS	2.0 (6.7)	-2.0 (6.0)	8.8 (8.9)
CALVES	-17.3 (3.6)	-13.4 (3.1)	-2.3 (3.3)
TOTAL	-18.7 (11.9)	-21.9 (7.8)	8.3 (14.5)

Large differences between counts in the same year were observed for the calf-to-hind ratio. In most years, Guinness et al. found calf-to-hind ratios of around 20 calves per 100 hinds, compared to the 30 to 40 calves per 100 hinds recorded by the DCS. Clutton-Brock and Albon (1991) have also noted this discrepancy in calf numbers. A two-way analysis of variance showed a significant difference between the three different counts for calves ($p=4.6 \times 10^{-5}$) only. Hind, stag and total counts were not significantly different. Missing values were not estimated and counts were log-transformed for this analysis.

On average, the DCS counted more animals than Guinness *et al.* which at least partly might be explained by the fact that the DCS counted in one area higher up which was not covered by the other counts. However, significant differences between DCS and both non-DCS counts were found for calves only and it seems justified to use this data set to attempt an estimate the precision of census counts. Visual inspection of plots of standard deviations of counts plotted against mean counts suggested a linear relationship between the two. Therefore the residual sums of squares from the two-way analysis of variance were used to calculate a coefficient of variation for stag, hind and total census counts (Table 3.2). The coefficients of variation for all three categories

were around twelve percent.

Table 3.2. Coefficients of variation (CV) for census counts in North Block of Rum based on Deer Commission and Guinness *et al.* census counts.

Category	CV (%)
Stags	12.8
Hinds	12.7
Total	10.7

3.2.2 Classification error in census counts

The variability in census counts performed by the Deer Commission for Scotland can be seen as arising from two sources: misclassification of animals into the three categories stags, hinds and calves, and errors in counting the total number of deer per group. Previously, misclassification in census counts has been studied using population reconstruction (Lowe, 1969; Clutton-Brock and Albon, 1989). The comparison of reconstructed population numbers and census counts does not distinguish between the two sources of variability. It also relies on correct ageing of dead animals as well as detection of all animals that died. The ageing of red deer by teeth inspection is difficult and variable (Lowe, 1967).

A study was carried out to assess the misclassification in census counts. The data collection took place during DCS's regular counting schedule. One experienced counter was assigned to act as verifier during a counting season. He accompanied a randomly selected counter, and made an independent assessment of the size and composition of

animal groups encountered. The verifier took more time classifying animal groups and in some cases went closer to the animal group counted than the counter or missed out some groups. The data come from census counts on 12 estates in 8 counting blocks (Figure 3.1) collected over a period of two years, 1994 to 1995.

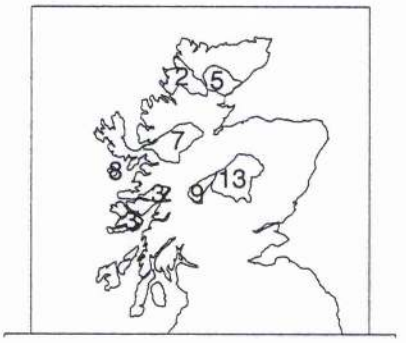


Figure 3.1. Counting blocks where verification took place. Numbers indicate the number of groups verified.

Overall data from 50 groups were collected. The size of groups verified varied greatly, with most groups having fewer than 20 animals (Figure 3.2).

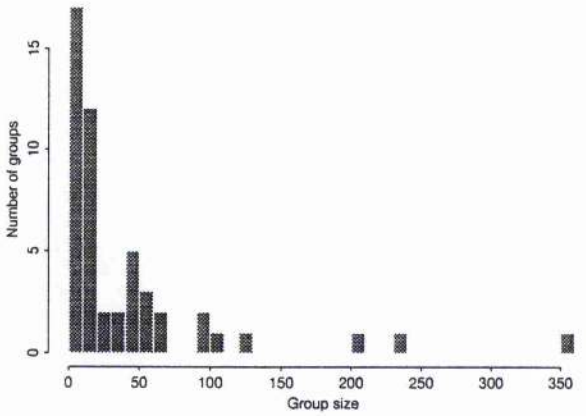


Figure 3.2. Histogram of group sizes verified.

Out of the 50 groups, in only five cases did the total number of deer counted for a

group by the verifier and the counter not agree. In four cases counts differed by only one animal.

The relationship of disagreement in group composition between the two counts and the size of the group verified was investigated. A new variable, agreement rate, was created which was assigned the value 1 if there was perfect agreement between the two counts and 0, if any of the sex and age categories disagreed. Figure 3.3 shows the relationship between the agreement rate and group size (verifier's count).The probability of perfect agreement was modelled by a logistic regression; it ranged from 84% for groups of size 5 to under 20% for groups of size 100.

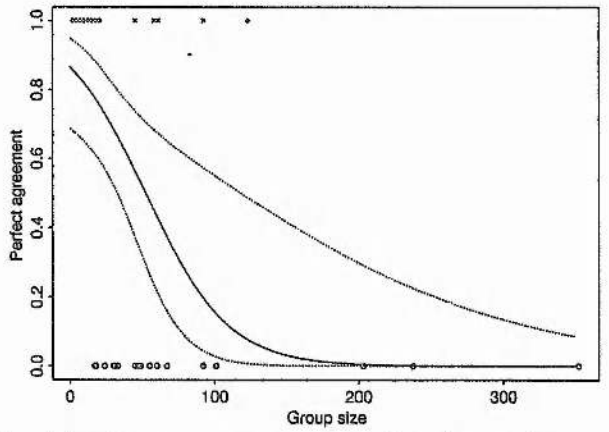


Figure 3.3. Classification agreement as a function of group size. Data (perfect agreement closed symbol; disagreement open symbol) and fitted relationship with 95% confidence interval (dotted line).

Using perfect agreement for the analysis is somewhat extreme as it does not take into account that larger groups are expected to be more likely to disagree. In contrast, the average relative classification error takes this into account. It is defined as the average of the difference between the counter's and the verifier's count divided by the verifier's count. The average relative classification error made by the counter assuming the

verifiers' counts are the true values were calculated for each age and sex category (Table 3.3).

Table 3.3. Average relative classification error made by counter assuming verifier's count is correct. Standard errors (s.e.) in brackets. No. groups is the number of groups containing at least one animal of the stated category.

Category	No. groups	No. of disagreeing groups	Average relative classification error [%] (s.e.)
Stags	43	9	-0.9 (0.16)
Hinds	38	14	-0.5 (0.10)
Calves	36	14	4.4 (0.61)

For stags, the average relative classification error was negative. This means that, on the assumption that the verifier's classifications are correct, on average counters recorded one stag too few for every 110 stags. For hinds, counters recorded one animal too few for every 200 hinds, and for calves, counters recorded one animal too many for every 23 calves.

Recorded errors in classification of stags and hinds were very small. The error rate for calves was rather higher. It seems likely that a few young stags and hinds tended to be classified by counters as calves. There might also be some confusion between young stags and hinds. Overall, stag and hind numbers were underestimated slightly, and calf numbers overestimated. Every attempt was made by the verifier to classify animals correctly. However, any bias in his classifications is likely to be in the same direction as for the counters, so these error rates are likely to be underestimates. Only five

groups with more than 100 animals were included in this study. It is these large groups that were most subject to mis-classification errors, so that larger errors than those quoted here can be expected for census counts involving many large groups. In order to assess the relevance of the results obtained here the distribution of group sizes verified was compared with the distribution of group sizes in a red deer population in North Ross counted in May 1995 (Figure 3.4). The majority of groups had fewer than ten animals, so that the conclusions drawn from this verification study might be assumed to apply to that population.

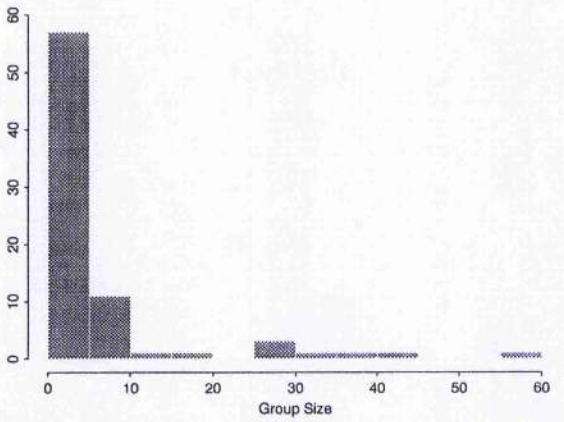


Figure 3.4. Distribution of group sizes in a red deer population in North Ross, May 1995.

There are other possible sources of errors for census counts not addressed in this study. They include bias in the verifier's counts and classifications; failure to detect all groups; counting of some groups more than once; and movements of animals in and out of counting blocks. Studies with different designs should be carried out to address these issues.

3.3 Feasibility study for aerial line transect method

3.3.1 Description of line transect method

Line transect methods are widely used for estimating animal abundance; they have been described by Buckland *et al.* (1993). Generally, a systematic grid of lines is randomly superimposed on the study area, and an observer travels along each line in turn, recording any animals detected. In the simplest case, all animals in a strip are counted, from which animal density is estimated as number of animals divided by area of strip. However, if the strip is sufficiently narrow to ensure detection of all animals within the strip is certain, many detected animals will be seen outside the strip, and so the method is inefficient. Instead, a much wider strip is allowed, and the perpendicular distance of each detected animal or, more commonly, group of animals from the line is estimated (Figure 3.5).

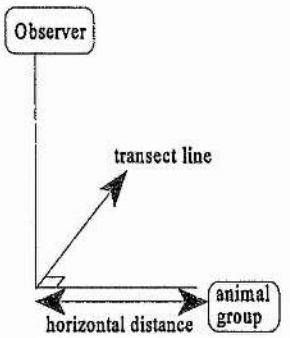


Figure 3.5. Schematic view of line transect method.

The perpendicular distances are used to estimate the density of animals in the study area. This is achieved by fitting a detection curve to the distances, which provides an

estimate of the probability an animal group is detected as a function of its distance from the line. Average group size in the population is estimated by modelling the sizes of detected groups as a function of probability of detection, and predicting mean group size when detection is certain. For this approach, the number of animal groups detected determines the precision of the final abundance estimate. In the aerial line transects reported on here, a helicopter was used for flying along the predetermined set of transect lines.

3.3.2 Study area and design

The study was carried out at the end of May 1995 in an area east of Ullapool, which is part of the Deer Commission for Scotland's counting block North Ross (Figure 3.6). A census count had been carried out in the same area at the beginning of April 1994 by a Deer Commission helicopter-based team and a ground-based team, both teams working simultaneously. The study area is about 280 km^2 and fairly flat with few forest plantations.

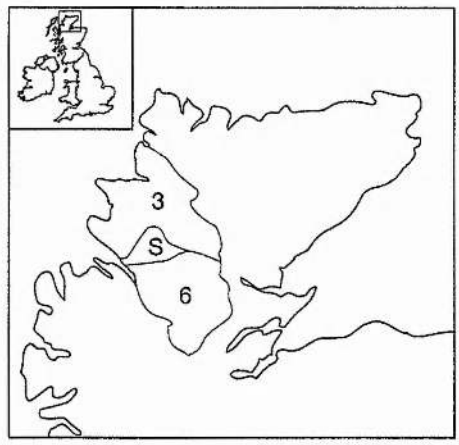


Figure 3.6. Map showing Deer Commission counting blocks West Sutherland (3) and North Ross (6) and the study area S, which is part of block 6.

The survey design consisted of a randomly placed grid of lines laid out in parallel in one direction and a second set of parallel lines perpendicular to the first set. Horizontal distances from the transect line to animal groups were measured with a Criterion 400 laser (Positioning Resources Ltd.) on one side of the line only. Group sizes were recorded, as was the composition of each group, i.e. numbers of stags, hinds and calves. For some groups, classification was not possible and their composition had to be estimated.

3.3.3 Estimation methods

Abundance estimation was carried out with the software package DISTANCE (Laake *et al.*, 1993). As the survey was one-sided, half (five) of the observations recorded as exactly on the transect line were excluded from the analysis. The key functions half-normal, hazard-rate and uniform were tried in combination with some adjustment terms to model the detection curve. The best approximating model was selected using Akaike's Information Criterion. Larger groups had higher probabilities of detection, so it proved necessary to adjust for this size bias in the analysis.

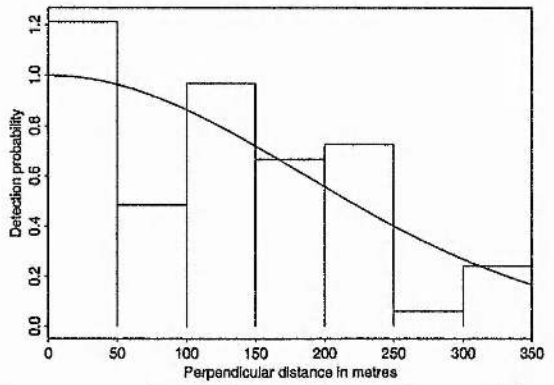


Figure 3.7. Histogram of red deer groups detected in the survey area at given perpendicular distances from the transect line and model fit for the half-normal detection function.

The half-normal model without further adjustment terms was selected for fitting the perpendicular distances in the data set comprising all groups (irrespective of their composition). This fit is shown in figure 3.7. Having obtained an estimate for the total number of deer in the study area, it was also of interest how many of these were stags, hinds and calves. If there is size bias in detection, and group composition changes with group size, the proportions of stags, hinds and calves in the sample will not correspond to the proportions in the population. However, the hind-to-calf ratio is unlikely to have a strong relationship with group size. Thus one solution is to calculate abundance estimates for hinds and calves, then calculate separate estimates for stags, i.e. split the data set into two: stags and others.

The group composition for unclassified groups was estimated as follows: fit a logistic regression to the proportion of stags in a group as a function of group size for classified groups; predict the number of stags for an unclassified group of known size using this model. Do the same for hinds and calves.

3.3.4 Abundance estimates

A summary of the line transect survey details is given in Table 3.4. The estimated density was 8.0 deer per km^2 with the 95% confidence interval spanning from 4.9 to 13.06 deer per km^2 (Table 3.5); this corresponds to a coefficient of variation of 25%. The mean group size in the population was estimated to be 4.05 animals, compared to an observed mean group size of 6.19.

Table 3.4. Survey details of the line transect survey in the study area.

Total length sampled [km]	167
Number of counters (excluding pilot)	4
Time taken to cover transects [h]	4
Travel time [h]	1
Study area [km^2]	280
Number of groups counted	77
Observed mean group size	6.19
% CV* of observed mean group size	19.20

* coefficient of variation

Table 3.5. Summary of analyses of the line transect survey data from the study area.

	Estimate	%CV*
Encounter rate [groups/km]	0.43	16.88
Effective search half-width [m]	218.07	23.19
Mean group size	4.05	14.43
Deer density [deer/km^2]	8.00	24.62
95% Confidence interval of density	4.9, 13.06	

* coefficient of variation

The line transect estimate of total red deer numbers is given along with the previous year's census in Table 3.6. The point estimate of 2240 agreed well with the census count of 2270 animals. The former had a 95% confidence interval of 1372 to 3656 animals; the census method provided no direct estimate of precision.

Table 3.6. Comparison of line transect estimate and census count of total numbers in study area.

Census in April 1994	Line transect survey in May 1995	
Total count	Total estimate	95% Confidence Interval
2270	2240	1372, 3656

Line transect estimates for stags and jointly for hinds and calves are shown in Table 3.7, together with the results from the census. The calf to hind ratio for the line transect method represents the observed average number of calves per hind. Large differences between the two methods are apparent. The line transect estimate for hinds and calves was rather imprecise due to the small number of groups in the survey which had animals in this category (31 groups). Fifty seven groups had one or more stags.

Table 3.7. Comparison of numbers of stags, hinds and calves from the aerial line transect method and the census method in study area.

	Census in April 1994	Line transect survey in May 1995	
		Estimate	95% Confidence Interval
Stags	964	1297	782, 2152
Hinds and calves	1306	938	446, 1976
Calf to hind ratio	0.22	0.44*	

*Observed average

3.3.5 Improving the aerial line transect method

Increasing the precision of the abundance estimate for the same effort can be achieved in two ways. Firstly, increasing the area of search; surveying both sides of the transect line will double the area of search, but it will require two survey lasers and five instead of four people. Secondly, increasing the survey speed; using a Global Positioning System (GPS), in which the coordinates of the transect lines can be stored in advance, will help to speed up the survey. Anthony and Stehn (1994) have written a computer program to facilitate the use of GPS systems in line transect surveys. Furthermore, classifying animals only up to 50 m on either side of the line would increase the survey speed. The desire to classify animals, especially larger groups, slowed down the survey. Almost all groups will be detected up to a distance of 50 m; at larger distances detection was found to be biased in favour of larger groups, which typically have a different age and sex composition than smaller groups.

The experience with the survey laser was very encouraging. The laser measured horizontal distances up to about 310 m through an open window and proved to be very valuable as it is difficult to estimate horizontal (ground) distances from a helicopter. The capability of the helicopter to stop almost instantaneously or to move up and down quickly was essential to the success of the survey.

Increased precision of the abundance estimate, which corresponds to a reduction of the coefficient of variation to about 10%, is anticipated if some of the suggestions for improvement of the method are implemented. Reducing the CV from 25% to 10% means increasing the area that has to be covered by a factor of 6.25. In the study 25

groups were detected within a distance of 50 m from the transect line; with an average group size of four animals this amounts to 100 animals. Thus, in a survey that aims at an abundance estimate with a CV of 10% about 625 animals would be expected to be detected and classified within 50 m of the transect line. If effort is not a limiting factor, the coefficient of variation of abundance estimates can be reduced to the desired level by simply increasing the effort. However, for small populations the line transect method is of limited value, as it might prove necessary to detect more animals than are present (by surveying areas more than once) to achieve the specified precision.

3.3.6 Assessment of feasibility study

The estimates of total population size from the line transect and the census methods agreed well, bearing in mind they denote populations in consecutive years. Precision for the line transect estimate was low with a coefficient of variation of 25%. In comparison, a coefficient of variation of 10.7% was estimated for total census counts from repeated counts made in the North block of Rum (Section 3.2.1). Even a coefficient of variation of 10% can give a rather large 95% confidence interval for the estimate of the total number of red deer. As an illustration, the 95% confidence interval for the aerial line transect estimate of the total number of red deer in the study area with a CV of 10% would be 1835 to 2735 animals.

Line transect estimates for stags and jointly for hinds and calves differed considerably from the census results. However, due to large uncertainty in the line transect estimates, this difference was not significant. A big difference occurred between the average calf-to-hind ratio observed in the survey and the ratio found in the census. This

might have several explanations. Conducting the line transect survey at the end of May was not the best timing to distinguish calves from adults, and stags from hinds. Calves are nearly a year old and easily confused with adults. The change from winter into summer coat makes hinds difficult to distinguish from stags. Furthermore, calf-to-hind ratios of the census and the aerial survey are less comparable as they were carried out in different years and calving rates vary from year to year. Nevertheless, this study indicates the potential of line transect methodology not only for obtaining a total estimate of deer numbers but also for demographic information, provided surveys are carried out at a time when different sex and age groups are easily distinguished.

The pros and cons of line transect methodology as applied to estimating red deer numbers in Scotland are summarised in Table 3.8. The analysis of the line transect data is very straightforward using the DISTANCE package (Laake *et al.*, 1993) and should not take more time than preparing data from the census count.

Table 3.8. Pros and cons of aerial line transect methodology for assessing red deer numbers when compared with current Deer Commission census methods.

Pros	Cons
More surveys for fixed costs	Precision poor in small areas
Precision quantified	No estimate available for individual
Need only few days of good weather	estates in general
No reliance on snow to push animals off the hills	

Line transect methodology has its greatest potential in large areas, with relatively small

scattered animal groups. The aerial line transect method would need only a few days of suitable weather, an important advantage when bad weather and the lack of snow often restrict the extent of census counts in any one year. The aerial line transect method as described here is most suitable for habitats where detection of animals on the transect line is certain. Whilst thermal imagers may help to ensure that detection along the track line is certain, in closed habitats such as forest, line transect surveys generally must be carried out on foot.

3.4 Cost benefit analysis of aerial line transects vs. census counts

The use of aerial line transect methodology for counting red deer in Scotland was investigated by comparing its costs with the cost of traditional ground based census counts. Two DCS counting blocks, West Sutherland and North Ross (see Figure 3.6), were chosen for the comparison. In both areas a census had been carried out recently. In West Sutherland 8.4 deer per km^2 were counted in 1990; for North Ross the figure was 9.6 deer per km^2 in 1994. The area accessible to red deer is about 1120 km^2 in West Sutherland (RDC, 1992) and 1258 km^2 in North Ross (Clutton-Brock and Albon, 1989).

For the line transect method, the number of deer groups present in an area affects the number of groups seen during the survey, which in turn determines the precision of the final line transect estimate. The more transect line, the more precise is the estimate obtained for a given density of animal groups, but the more expensive is the survey. Fixing the precision, measured by the coefficient of variation, of the abundance estimate at a certain level allows calculation of the necessary length of transect line and thus the

resources needed to cover it. The calculation of the length L of transect line for the desired coefficient of variation $CV(\hat{N})$ was carried out based on formulae given in Buckland *et al.* (1993):

$$L = \frac{n_0 \ (CV(\hat{D}))^2 + \{\hat{se}(\hat{E}(s)) \ \sqrt{(n_0)} \ / \ \hat{E}(s) \ \}^2}{\frac{\hat{N} \ 2 \ \hat{\mu}}{A \ \hat{s}_A} \ CV(\hat{N})^2} \qquad (3.1)$$

where n_0 is the number of groups counted in the study area, $CV(\hat{D})$ is the coefficient of variation of the density of groups in the study area and $\hat{se}(\hat{E}(s))$ is the standard error of the estimated mean group size $\hat{E}(s)$. The effective search half-width is μ. These calculations are carried out for an area of size A, with an estimated total red deer population of size $\hat{N}$ in groups of mean group size s_A.

In contrast to the line transect study (Section 3.3), it was assumed here that both sides of the transect line are surveyed. Average group size of red deer was assumed to be six, which is slightly higher than was estimated in the study area and therefore gives a conservative estimate of the length of the transect line necessary for a given precision. A coefficient of variation CV of 10% was regarded as a desirable level of precision for a line transect estimate, which is close to the CV of 10.7% achieved in repeat counts on Rum. Cost and effort analyses were carried out for obtaining red deer estimates in both counting blocks separately as well as combined. Table 3.9 lists the information used for the calculations. The one-off costs of material necessary for the line transect method such as survey lasers and a GPS system were ignored here.

Table 3.9. Data used for cost comparison between aerial line transect method and ground-based census method.

Line transect survey	
Effective search half-width [m]	218
Mean group size	6
Survey speed [km h^{-1}]	42
Length of helicopter counting day [h]	5
Size of helicopter counter team [persons]	5
Helicopter cost [£ h^{-1}]	650
Census count	
Subsistence per day [£ day^{-1} $person^{-1}$]	60
Size of census counter team [persons]	10
Transport cost [£ day^{-1} $person^{-1}$]	50
Line transect survey and Census count	
Salary [£ day^{-1} $person^{-1}$]	100

Estimated costs for an aerial line transect abundance estimate with a 10% CV and for a census count, are summarised in Table 3.10. Half the number of people are required for fewer days to carry out a line transect survey instead of a census count. For West Sutherland, a line transect estimate of deer numbers would cost 77% of a census count. In North Ross the line transect estimate would cost 58% of a census count and take about 33% of the time.

Table 3.10. Comparison of costs and effort for aerial line transect (LT) abundance estimation (10% coefficient of variation) and ground-based census counts for different counting blocks in Scotland.

	West Sutherland		North Ross		West Sutherland and North Ross	
	LT	Census	LT	Census	LT	Census
Transect line [km]	714	-	626	-	665	-
Survey time [h]	17	-	15	-	16	-
Travel time [h]	4	-	4	-	4	-
Total number of days	4	10	4	12	4	22
Total person days	20	100	20	120	20	220
Cost counters [£]	2 000	10 000	2 000	12 000	2 000	22 000
Cost helicopter [£]	13 700	-	12 300	-	12 900	-
Cost transport [£]	-	5 000	-	6 000	-	11 000
Subsistence [£]	-	5 400	-	6 600	-	12 000
Cost external [£]	13 700	10 400	12 300	12 600	12 900	23 000
Total cost [£] (counters + external)	15 700	20 400	14 300	24 600	14 900	45 000

The calculations for a combined estimate of red deer in West Sutherland and North Ross demonstrate the great potential of the aerial line transect method for large areas. Whereas the costs of a line transect survey are almost unchanged, census costs increase if the area increases. For about 33% of the resources required for a ground based census of this combined area, a line transect estimate can be obtained. It would only take about 18% of the time of a census.

3.5 Simulation study of the effects of abundance estimation error

In the previous section it was assumed that an abundance estimate with a coefficient of variation of 10% would be sufficient for practical purposes. However, no results are available for judging whether this assumption is reasonable. The required precision will depend on the intended use of the abundance estimate. One possible use of abundance information could be to estimate population trends in order to find out whether a population was increasing, decreasing or stable. Bayesian trend estimation is a suitable method to do this. It has been used to estimate the population growth rate of an eider duck population in order to find out whether this population should be classified as endangered (Taylor *et al.*, 1996).

In Bayesian trend estimation the Bayesian approach of parameter estimation is applied to time series of observations for obtaining estimates of population trends. Consider the exponential population model

$$N_{t+1} = N_t \, e^{r} \tag{3.2}$$

to describe the growth of a population with N_t being the total number of animals at time t and r the net population growth rate. Trajectories of populations based on the exponential model (3.2) are entirely determined by the size of the population at time 0, N_0, and the growth rate r, which is the parameter of interest. Hence the unknown parameters to be estimated are $\theta = \{r, N_0\}$. Assume that observations or estimates of the population size at time t, denoted as y_t, are available which have been obtained with known variance V_t. The conditional likelihood for the unknown parameters r and N_0 given all T available population size estimates is

$$\mathfrak{L}(N_0, r|y_t) = \prod_{t=1}^{T} \mathfrak{L}(N_t|y_t) = \prod_{t=1}^{T} p(y_t|N_t) \tag{3.3}$$

Assuming a normal distribution for the observed number of animals at time t, $(y_t|N_t) \sim N(N_t, V_t)$ each element of the right hand side of the conditional likelihood function (eq. 3.3) is written as

$$p(y_t|N_t) = \frac{1}{\sqrt{2\pi V_t}} \exp(-\frac{(y_t-N_t)^2}{2V_t}) \quad (3.4)$$

Prior distributions $p(\theta)$ are defined for all unknown parameters. The joint posterior distribution of θ is obtained through Bayes theorem. Taking a sampling-resampling approach for carrying out the integration (Smith and Gelfand, 1992), a sample of size n is drawn from the prior parameter distributions $p(\theta)$ to give the set $\{\theta_1,...,\theta_n\}$. For each θ_i, $0<i<n+1$, the standardised likelihood value is calculated. Point estimates for the posterior parameter values are obtained as weighted averages using the sample from the prior distributions and the standardised likelihood weights.

A simulation study was carried out to address the question of how uncertainty in population size estimates might influence the estimates of the population growth rate r. The simulations were carried out as follows.

1. Simulate population for T years ($1<T<11$) using the exponential model (3.1) with population growth rate $r = \{-0.1, -0.05, 0, 0.05, 0.1\}$ and $N_0=1000$;

2. For simulated populations estimate population abundance in each year by drawing independent random samples from Normal distributions with mean equal to population size and coefficient of variation $c = \{0, 5, 10, 20\}$ percent;

3. Use Bayesian trend estimation to obtain point estimates for the population growth rate.

4. Repeat steps 2 and 3 for 10 iterations.

5. Repeat steps 1 to 4 for time series of population data and abundance estimates of

different lengths, $T = 2,..., 10$.

For all simulations, the prior distribution for N_0 was assumed to be uniform, 0.7 to 1.3 times the abundance estimate at time 0. The prior distribution for the population growth rate was uniform(-0.15, 0.15) and the number of simulations 1000. The abundance estimation variance V_t was assumed to correspond to a coefficient of variation of 10%. Point estimates of the population growth rate were assessed by looking at the estimation variance and the average squared prediction bias based on 10 iterations.

The main effect of abundance estimation error was to increase in the variance of point estimates of the population growth rate r (Figure 3.8). The actual size of the variance of point estimates varied somewhat depending on the true growth rate but similar overall patterns were observed. If two to four abundance estimates were used, a coefficient of variation of 10% for the abundance estimation error resulted in similar variances compared to smaller abundance estimation errors whereas a coefficient of variation of 20% led to much larger variances. However, if at least five abundance estimates were available, the differences in the variance of point estimates of the population growth rates nearly disappeared and all variances became similar. This might be due to the assumption of a fixed 10% estimation error used in the estimation process which led to similar variances of point estimates when more than four abundance estimtes were used whatever the true abundance estimation error.

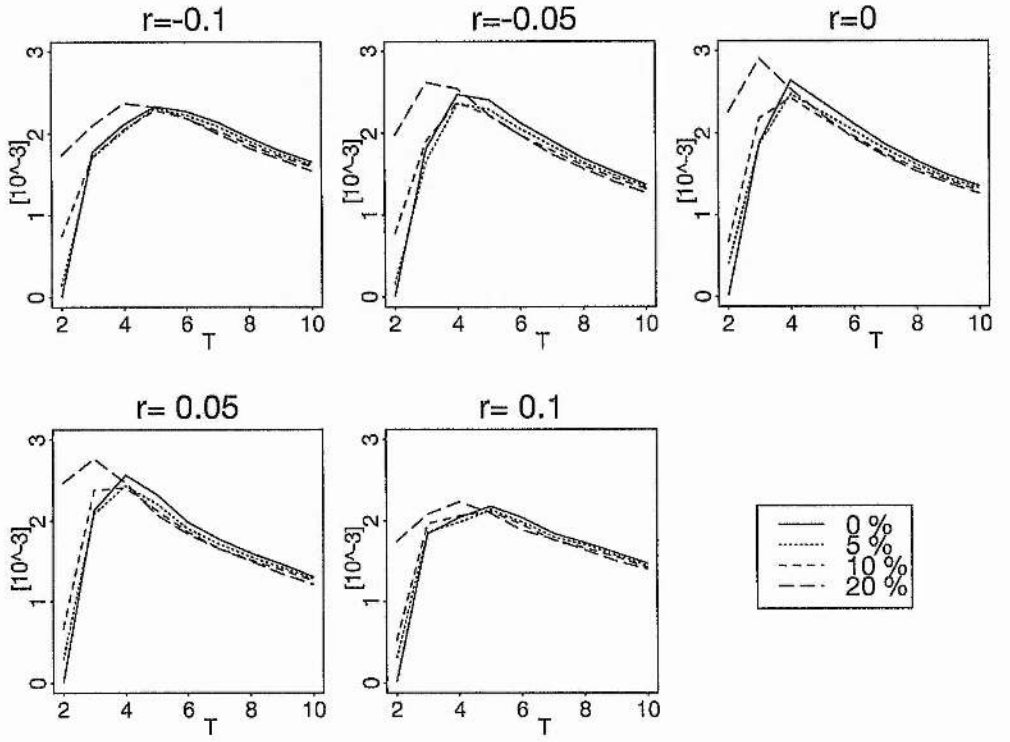


Figure 3.8. Variance of point estimates of population growth rates for different true growth rates, various levels of abundance estimation error (% CV) and different numbers of abundance estimates *T*.

The results for the average squared bias of point estimates of the population growth rate were similar to those for the variance (Figure 3.9). When only two data points were used, the average squared bias resulting from the use of abundance estimates with no estimation error (0% in Figure 3.9) was nearly as large as for cases with larger estimation errors; it was slightly larger when more than two data points were used. It took at least seven abundance estimates before the average squared bias was approaching zero.

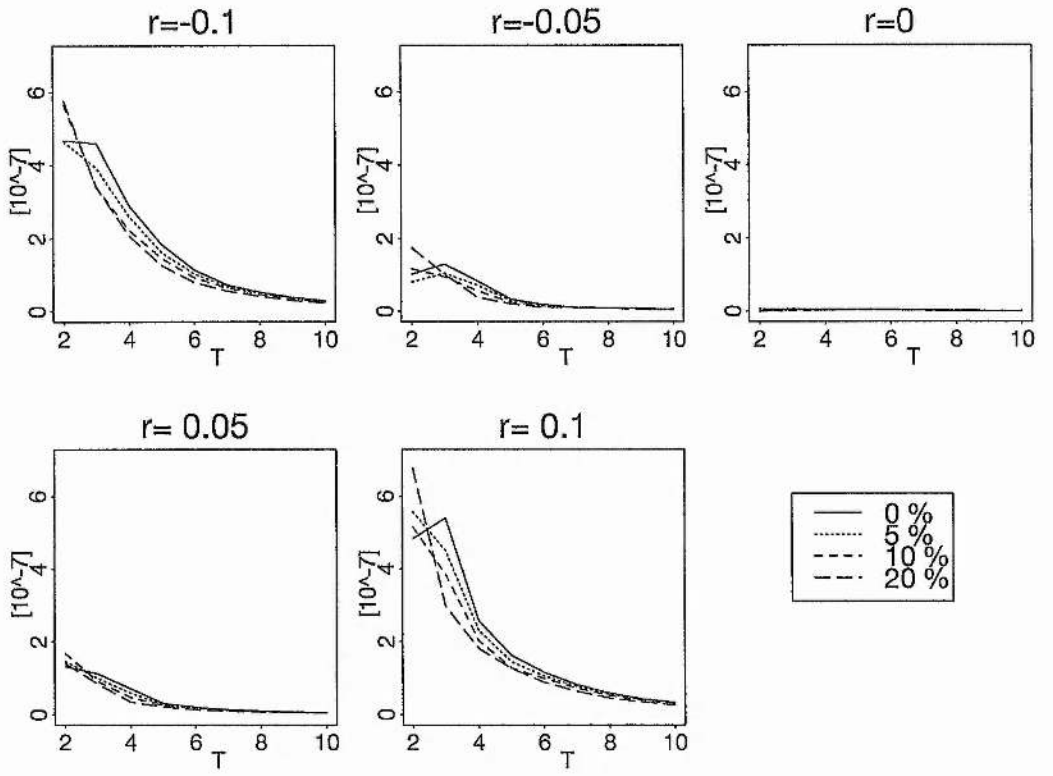


Figure 3.9. Average squared bias of the point estimates of population growth rates for different true values, various levels of abundance estimation error (% CV) and different numbers of abundance estimates T.

These simulations seem to suggest that the variance of point estimates of the population growth rate based on abundance data with 0 to 10% coefficients of variation was rather similar. When at least five abundance estimates were used, the size of the coefficient of variation of the abundance data (in the 0 to 20%) became unimportant. Similar results were obtained for the average squared bias of point estimates.

3.6 Discussion

In this chapter counting methods for red deer on open hill land were studied. The traditional method of choice, census counting, was assessed with respect to precision and classification error. In repeated census counts on Rum, coefficients of variation between eleven and thirteen percent were found for stag, hind and total counts. Calf counts were more variable. This study tried to quantify the variation in census counts by comparing three repeat counts carried out in a short interval of time by two different parties. It does not provide any information about the accuracy of census counts. In areas other than Rum, movement of deer between counting blocks and into and out of woodland within a counting block, as well as other factors may well lead to an effective coefficient of variation greater than 10%.

A study was presented that looked at the classification of animals into the groups stags, hinds and calves by comparing two independent counts. Generally, for groups containing more than 150 animals a discrepancy in the total counted by the counter and the verifier is expected to be found. In this comparison, the mean relative classification error for stags as well as for hinds was negative and under one percent. Calf counts had a mean relative classification error of 4.4 %. In order to calculate correction factors for the classification into age and sex groups of red deer census counts more groups from different areas would have to be verified, ensuring that the proportion of different group sizes in the sample are similar to those in the population for which the correction factors are required. Using the results of the study as an indication for the magnitude of misclassification errors to be expected in census counts, it seems however, that misclassification is only a minor contributor to counting errors compared to the

variability estimated for repeated counts on Rum or the unquantified problem of missing altogether groups of animals dwelling in forests.

To test the feasibility of alternative methods to census counts in Scotland, a study using aerial line transect methodology was successfully carried out. A coefficient of variation of only 25% was achieved for the abundance estimate due to a number of practical constraints. Ways of improving the method were identified and would have to be tested in practice to see whether the predicted improvements in precision could be achieved. In line transect methodology the precision of the final estimate depends on the number of groups sampled, not the proportion of groups seen. As a consequence, the method offers substantial gains over census counts when the area to be covered is large (adding to the expense of a census count) or when the study population comprises a large number of animal groups (so that the required number of detections for a given precision is readily obtainable). Conversely, if the study population is small, and easily censused, there is little merit in carrying out a line transect survey. This was demonstrated by looking at the costs of estimating red deer numbers in three different areas with both census and aerial line transects methods. Thus, aerial line transect methodology seems to be a competitive alternative to census counts, especially when the required precision of the estimate is not too large and no local estimates are required. It has to remembered however, that both methods have a number of drawbacks in common. For example, animals in woodland cannot be estimated using the aerial line transect method unless it is open woodland or young plantations. Steep countryside poses practical problems. Hence, there is scope for evaluating other counting methods which do not suffer the same limitations. The change-in-ratio method was identified as a promising method, but for practical reasons it was not possible to

carry out an evaluation study. A study looking at the change-in-ratio method, especially in conjunction with the problem of red deer in woodland would make a welcome contribution to the problem of red deer management which relies on having reliable abundance estimates.

A simulation study was carried out to investigate the effect abundance estimation error might have on the variance and squared bias of population trend estimates. In this study this effect was most marked if only two or three abundance estimates were available to base the Bayesian trend estimation upon. For the cases investigated, it was found that not much was gained in terms of reduction in estimation variance and squared bias by reducing the coefficient of variation of abundance estimates to less than 10%. The simulation study also highlighted the interaction between the amount of data (the number of abundance estimates) and the precision of those estimates (the coefficient of variation in this case). More data can make up for lower precision. The question of a suitable precision of abundance information should be considered in conjunction with the frequency of abundance estimates and the use they are put to.

Chapter 4 Monitoring trends in red deer numbers

4.1 Introduction

In recent years, pressure for increasing the red deer cull in Scotland, especially hinds, has been exercised by the Deer Commission for Scotland in order to control red deer numbers (e.g., RDC, 1996). Estimates of total deer numbers and population trends would make it possible to assess how effective this culling program was and if required would provide evidence to support more drastic measures.

Different methods for directly assessing red deer numbers in a given area have been reviewed in chapter 3. On a larger scale, for example the whole of the open hill land in Scotland, none of these methods is practically feasible. Hence, for monitoring total red deer numbers on the open hill in Scotland statistical modelling has a role to play. The choice of counting method will be important only in so far as its precision will have an impact on the estimates of total deer numbers.

One source of information to base the estimation of total red deer numbers upon are the census counts that have been carried out in late winter and spring by the Deer Commission for Scotland in discrete counting blocks since 1959. The counting blocks were set up to contain enclosed populations with little movement between blocks (Stewart, 1976). Of the 49 counting blocks that were originally defined, 39 have been counted at least once by 1995, twice in recent years two blocks were combined and one new block was created.

The count and cull information from 1970 to 1995 only was used in the analysis as cull information before 1970 was incomplete. Even so for some blocks cull information was missing for the early 1970's in which case the average of the first two years for which data were available was used. On average, 4.7 blocks (range 2-8) were counted per year between 1970 and 1995 (Table 4.1). Most blocks were counted once or twice during this 26 year period (Table 4.2). The most notable exception is the Isle of Rum which has been counted nearly every year as part of an ongoing research programme.

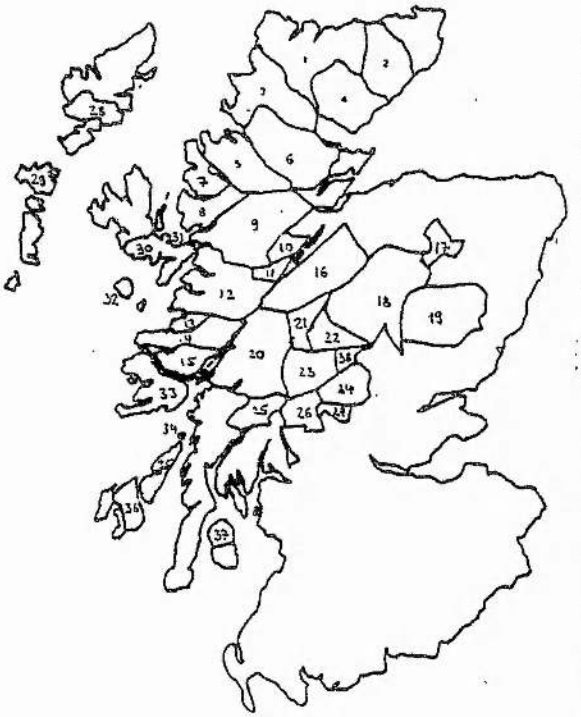
Table 4.1. Number of counting blocks counted in each year by DCS.

Year												
70	71	72	73	74	75	76	77	78	79	80	81	82
4	4	5	2	5	5	4	3	6	8	6	2	5
83	84	85	86	87	88	89	90	91	92	93	94	95
4	3	4	6	5	6	5	4	5	4	4	8	4

Table 4.2. Frequency of times counting blocks have been counted by DCS between 1970-95.

Number of counts	Number of counting blocks
1	7
2	16
3	5
4	5
5	1
6	2
7	1
23	1

The blocks for which counts were available for analysis are shown in Figure 4.1 below. All blocks have been grouped into 7 regions (see figure 2. 1). These regions have been defined for management purposes by the Association of Deer Management Groups (R. Cooke, pers. comm.).



Region	No	Name	Region	No	Name
1	1	North Sutherland	6	20	Ben Nevis-Blackmount
1	2	Caithness	3	21	Courrour-Ben Alder
1	3	West Sutherland	3	22	East Loch Erich
1	4	East Sutherland	6	23	Rannoch
2	5	West Ross	6	24	South Loch Tay
2	6	North Ross	6	25	Inverary-Tyndrum
2	7	Gairloch Conservation Unit	6	26	Balquhidder-Trossachs
2	8	Applecross & Shieldaig-Ledgowan	6	27	Glenartney
2	9	South Ross	7	28	Harris-Lewis
2	10	Glenmoriston	7	29	North Uist
3	11	Ardochy-Port Clair	7	30	Skye
5	12	West Inverness-shire	7	31	Scalpay
5	13	West Loch Shiel	7	32	Rum
5	14	Ardnamurchan & Conaglen-Ardgour	7	33	Mull
5	15	Morvern	7	34	Scarba
3	16	Monadhliaths	7	35	Jura
4	17	Cabrach-Glenfiddich	7	36	Islay
4	18	Cairngorms-West Grampians	7	37	Arran
4	19	East Grampians	6	38	Strathtay

Figure 4.1. Map of Scotland with counting blocks which were included in the analysis. The table gives the number and region for each counting block.

Previously, Clutton-Brock and Albon (1989, Appendices 2 to 4) have used the DCS counts to model red deer densities in Scotland using regression models which included effects due to year, counting block, and parish within block. They fitted separate models for total deer, stag and hind densities and found no evidence for any block-year interactions. Having fitted the models (which included polynomial time trends for smoother results), they obtained estimates of deer densities in all geographical units (blocks and parishes) and explored links between deer densities and other explanatory variables using regression techniques.

In this chapter the DCS's census and cull data were analysed for estimating the total number of red deer on the open hill in Scotland for the years 1970 to 1995. A simple population model was formulated that in addition to year and region effects included natural changes and the changes in deer densities due to culling. Ultimately, an estimate of the total number of deer on the open hill in Scotland was sought, but initially the numbers of deer in individual counting blocks were estimated.

4.2 Model

The processes affecting the size of a red deer population are natural mortality, birth and culling. Mortality and recruitment can be combined into a net population change rate. To eliminate some of the variation between counting blocks due to different block sizes a model for deer density rather than deer numbers was formulated. The area of each counting block used in the analysis corresponds to the total area including parts which are not accessible to red deer.

A simple state space model for the density of a population in counting block i in the spring of year t+1 as a function of its density in the spring of year t can be written as

$$D_{i,t+1} = \phi_{i,t} D_{i,t} - C_{i,t} + \varepsilon_{i,t} \quad (4.1)$$

where $D_{i,t}$ is the total density of deer in the ith block at the time of the census (spring) in year t; $\phi_{i,t}$ is the net population change rate and $C_{i,t}$ is the number of stags, hinds and calves culled divided by the size of the ith block, i.e. number of adult animals culled per km^2. The cull is assumed to have no error. This formulation of the model assumes that natural mortality and recruitment depend on the density of animals in spring rather than the density after the cull. It also presupposes additivity of natural and culling mortality. The state error is assumed to be $\varepsilon_{i,t} \sim N(0, \sigma^2 D_{i,t}^2)$, which implies a constant coefficient of variation. Spatial correlations between, and temporal correlations within, counting blocks are assumed to be zero, thus $Corr(\varepsilon_{i,t}, \varepsilon_{i',t}) = 0$ for $i \neq i'$ and $Corr(\varepsilon_{i,t}, \varepsilon_{i,t'}) = 0$ for $t \neq t'$.

The net population change rate $\phi_{i,t}$ is assumed to be a function of time and geographical region. A possible form for this relationship is

$$\log(\phi_{i,t}) = \mu + \psi_j + \theta_t \qquad i \in R_j \quad (4.2)$$

where the overall mean of the net change rate is μ; $\psi_j \sim N(0, \sigma_1^2)$ is the effect of region j in which block i lies; R_j is a set with the counting block numbers of region j and $\theta_t \sim N(0, \sigma_2^2)$ is the effect of year t. Note that no region-year interaction is modelled because counts were not available in every year for all regions. Region effects will contain differences between regions due to soil types, vegetation and other factors. Due to the scarceness of data, a region rather than block effect was chosen. Assuming this structure for the net change rate means that blocks with only one count can be included in the analysis.

The DCS counts are observations which are assumed to have been obtained with some random error. Hence the observation equation for the counts observed per unit area in block i in year t, $Y_{i,t}$, can be expressed as

$$Y_{i,t} = D_{i,t} + \omega_{i,t} \tag{4.3}$$

with observation error $\omega_{i,t}$. The observation error is due to miscounting and missing animal groups and was set to be Gaussian with the variance proportional to the square of the deer density, $\omega_{i,t} \sim N(0, \nu^2 D_{i,t}^2)$. Hence, a constant coefficient of variation ν was assumed for all counting errors based on the study of repeat counts on Rum (section 3.2.1).

4.3 Estimation methods

4.3.1 Background

For parameter estimation in state space models one of two approaches is commonly chosen: the Kalman filter and its extensions or Markov chain Monte Carlo (MCMC) methods. The estimation of net population change rates and red deer densities has been tried with both methods.

For linear models, known model parameters and Gaussian errors, the classical Kalman filter provides an estimate for the state variables conditional on the observations up to a certain point in the time series (Meinhold and Singpurwalla, 1983). The Kalman filter has been used extensively, especially for the analysis of econometric time series (e.g. Harvey, 1989) and in fisheries management (Sullivan, 1992; Freeman and Kirkwood, 1995). In cases when the regression parameters of the linear state equation are

unknown, these can be estimated by maximum likelihood for example via the EM algorithm (Shumway and Stoffer, 1982). The model (4.1) is linear for fixed net population change rate $\phi_{i,t}$ and both state and observation errors are assumed to be Gaussian though the observation error is assumed to depend on the observations but not on the state. If the observation error depended on the state, the classical Kalman filter would not be applicable but an extension of it, the generalised Kalman filter (Zenwirth, 1988) would then apply. As already mentioned, the EM algorithm (Dempster *et al.*, 1977) is often used for carrying out the parameter expectation, where the estimation step (E-step) gives estimates for all state variables. In the maximisation step (M-step) conditional on the state, maximum likelihood estimates for all model parameters are obtained. For many formulations of state space models analytical results can be obtained for use in the maximisation step.

Initially, the Kalman filter was used for estimating deer densities using a state space model which contained separate net population change rates ϕ_i for each block which were assumed to be fixed over time. However, convergence of the Kalman filter could not be reached and results depended very much on starting conditions. It was concluded that this was due to the sparseness of counts for many blocks and that more restrictive models had to be formulated, for example by assuming a regional population change rate. The change from a fixed effects to a random effects model for the net population change rate as given in (4.2) offered a way of modelling regional as well as temporal effects given the restricted information. The estimation of such models seemed to be more easily carried out by MCMC, hence the Kalman filter was abandoned in favour of MCMC methods.

MCMC methods are a broad class of estimation methods based on Monte Carlo simulation which have been employed for time series as well as spatial data analysis. The Gibbs sampler algorithm (Geman and Geman, 1984) is an MCMC method which can be regarded as a stochastic counterpart to the deterministic EM-type algorithms (see table 5 in Meng and van Dyk, 1997 for the equivalent Gibbs sampler method for a number of EM-type algorithms). The Gibbs sampler algorithm is often used in Bayesian computations for obtaining samples from the posterior distributions (e.g., Gelfand and Smith, 1990; Smith and Roberts, 1993; Wakefield *et al.*, 1994; Carter and Kohn, 1994; Craig *et al.*, 1997). In the Gibbs sampler, the expectation and maximisation steps of the EM-algorithm are replaced by random draws from conditional distributions. This makes the exploration of different models straightforward compared to EM-type algorithms which work with analytical formulations. Reviews of Markov chain Monte Carlo methods, in particular the development and use of the Gibbs sampler in many fields of application, have been provided for example by Smith and Roberts (1993) and Besag and Green (1993). Tierney (1994) gives a theoretical account of MCMC methods.

4.3.2 Markov chain Monte Carlo methods

Description

Suppose we are interested in a sample from the distribution $\pi(x)$ for $x \in X$, for example the posterior distribution in Bayesian inference, but cannot sample from this distribution directly. The general principle of Markov chain Monte Carlo methods is to construct a Markov chain whose equilibrium distribution is equal to $\pi(x)$ and has state

space X. Any random variable which can take values equivalent to identifiable states within a state space X and non-zero probabilities q to go from one state to another can be regarded as a Markov chain. Many time variant processes fall into this category. For example, the number of animals in a counting block is a Markov chain which is in a different state at each observed time point, i.e. each year at the time of counting. A number of algorithms exist to construct Markov chains with the required equilibrium distribution. The Gibbs sampler is a popular algorithm for multivariate problems. Another common algorithm is the Hastings algorithm (Hastings, 1970) which is often carried out within the Gibbs sampler.

Assume x is a vector with k elements x_1 to x_k. The Gibbs sampler produces a random sample from the distribution $\pi(x)$, $x=\{x_1,...x_k\}$, by repeatedly sampling from the conditional distribution of x_i given all other elements of x, $\pi(x_i|x_{<i}, x_{>i})$. At step 0 of the Gibbs sampler, an arbitrary sample $x^0=\{x^0{}_1,...,x^0{}_k\}$ is selected for all elements of x. At the next step, a new value for element one, $x^1{}_1$, is selected from $\pi(x_1|x^0{}_{>1})$, for element two, $x^1{}_2$ from $\pi(x_2|x^1{}_1,x^0{}_3,...,x^0{}_k)$ and so on for all k elements of x. After s steps of the Gibbs sampler, the series $x^0...x^s$ is a realisation of a Markov chain. Introducing the Metropolis-Hastings algorithm (Metropolis *et al.*, 1953; Hastings, 1970) into the Gibbs sampler can make the sampling of the state space X by the Markov chain $x^0...x^s$ more efficient and is essential when sampling from the full conditional distributions is impossible or tedious. Instead of sampling directly from the full conditional distribution $\pi(x_i|x^j_{<i}, x^{j-1}_{>i})$ at step j of the Gibbs sampler, a new value x^j_i is accepted for element i with probability $\min(r, 1)$ where r is

$$r = \frac{\pi(x_i' | x_{<i}^{j}, x_{>i}^{j-1})\ q(x_i', x_i^{j-1})}{\pi(x_i^{j-1} | x_{<i}^{j}, x_{>i}^{j-1})\ q(x_i^{j-1}, x_i')}, \qquad (4.4)$$

$q(x_i^{j-1}, x_i')$ is the probability of sampling a new value x_i' given the previous value x_i^{j-1}; it is also referred to as a transition probability. If $q(x_i^{j-1}, x_i') = q(x_i')$, that is a test value x_i' is always drawn from the same distribution, the chain is called an independence chain. The original Metropolis algorithm assumes that $q(x_i^{j-1}, x_i') = q(x_i', x_i^{j-1})$, which is optimal among a wide range of choices (Tierney, 1994).

Asymptotically the Gibbs sampler gives a sample from the required distribution $\pi(x)$. Different diagnostic techniques have been developed for analysing the samples $x^0 \ldots x^s$ and for judging when to stop sampling, i.e. how large s should be. A summary of available diagnostic techniques is given by Cowles and Carlin (1996).

Conditional distributions

Here MCMC methods were used to estimate the parameters in the state and observation equations (4.1, 4.2 and 4.3). The set of parameters to be estimated is $\Omega = \{D_{1,1},\ldots,D_{38,26}, \mu, \psi_1,\ldots,\psi_7, \theta_1,\ldots,\theta_{26}, \sigma^2, \sigma_1^2, \sigma_2^2\}$ which has 1025 elements. Deer densities are estimated in 38 blocks (i =1,..,38) within 7 regions (j=1,..,.7) for 26 years (t=1,...,26). The coefficient of variation v of the counting error, (4.3), was fixed and set to 0.1 based on the study of repeat counts (section 3.2.1).

The aim is to estimate parameter Ω_m, m=1...1025, which is achieved by obtaining a sample from the conditional distribution $\pi(\Omega | Y^T)$ where Y^T denotes all densities of all

blocks in all years. The Gibbs sampler with Metropolis-Hastings step is set up to sample the conditional distributions $\pi(\Omega_m|Y^T,\Omega_{-m})$ in turn. The resulting Markov chain will be a (correlated) sample from the desired distribution. At each step j of the Gibbs sampler a new test value is accepted for Ω_m with probability $\min(r_m, 1)$ (4.4). The superscript j indicating the step of the Gibbs sampler has been dropped in the following description of conditional parameter distributions and transition probabilities.

Conditional distributions $\pi(\Omega_m|Y^T,\Omega_{-m})$ are required for all parameters. In the following these conditional distributions (based on equations 4.1, 4.2 and 4.3) are given. As the Metropolis-Hastings algorithm (4.4) is used, sampling probabilities $q(\Omega_m, \Omega'_m)$ are also specified. All sampling distributions were selected after some trial runs. The standard deviation of the sampling distribution influences the correlation between subsequent samples in the chain. If the standard deviation is too small, the autocorrelation is high and the acceptance rate for new values is high. Conversely, if the standard deviation is too large, the acceptance rate for new values is low. The chain is slowly mixing in both cases, that means the exploration of the parameter space is slow. Hence the choice of the sampling distribution is important but unfortunately it is rather subjective.

For the deer density in block i and year t, the conditional probability for test value $D'_{i,t}$ given the current values for the densities in year $t-1$ and $t+1$ and the count in the same year, is

$$\pi(D'_{i,t}|D_{i,t+1},\ D_{i,t-1},\ Y_{i,t}) = p(Y_{i,t}|D'_{i,t})\ p(D'_{i,t}|D_{i,t-1})\ p(D_{i,t+1}|D'_{i,t}) \qquad (4.5)$$

where

$(Y_{i,t}|D'_{i,t}) \sim N(D'_{i,t},\ v^2\ D'^2_{i,t})$ if there was a count and $p(Y_{i,t}|D'_{i,t}) = 1$ otherwise;

$(D'_{i,t}|D_{i,t-1}) \sim N(\phi_{i,t-1}D_{i,t-1} - C_{i,t-1},\ \sigma^2\ D^2_{i,t-1})$ if t>1 and $p(D'_{i,t}|D_{i,t-1}) = 1$ otherwise;

$(D_{i,t+1}|D'_{i,t}) \sim N(\phi_{i,t}D'_{i,t} - C_{i,t},\ \sigma^2\ (D'_{i,t})^2)$ if t<26 and $p(D_{i,t+1}|D'_{i,t}) = 1$ otherwise.

A new test value $D'_{i,t}$ is drawn from a Normal distribution centred on the current value with standard deviation $0.05*\bar{Y}_{i,.}$; $\bar{Y}_{i,.}$ is the mean count for block i. This means that the transition probabilities are equal, $q(D_{i,t},\ D'_{i,t}) = q(D'_{i,t},\ D_{i,t})$.

The conditional probability for a test value for the mean of the net change rate μ' is

$$\pi(\mu'|\sigma^2, \psi_j, \theta_t, D_{i,t};\ i\in R_j;\ j=1,...,7; t=1,...,26) = \prod_i \prod_t p(\frac{\varepsilon_{i,t}}{D_{i,t}}|\mu') \qquad (4.6)$$

with $(\frac{\varepsilon_{i,t}}{D_{i,t}}|\mu') \sim N(0,\sigma^2)$; $\varepsilon_{i,t}$ is the error in equation 4.1 and $i\in R_j$ denotes all blocks i that are part of region j. A new test value μ' is drawn from a Normal distribution centred on the current value with standard deviation 0.01, i.e. $q(\mu,\ \mu') = q(\mu',\ \mu)$.

For the effect of region j, the conditional probability for test value ψ'_j is

$$\pi(\psi'_j|\sigma^2, \sigma_1^2, \mu, \theta_t, D_{i,t};\ i\in R_j; t=1,...,26) = p(\psi'_j|\sigma_1^2) \prod_t \prod_{i\in R_j} p(\frac{\varepsilon_{i,t}}{D_{i,t}}|\psi'_j) \qquad (4.7)$$

with $(\psi'_j|\sigma_1^2) \sim N(0,\sigma_1^2)$ and $(\frac{\varepsilon_{i,t}}{D_{i,t}}|\psi'_j) \sim N(0,\sigma^2)$. A new test value is drawn from a normal distribution with mean equal to the current value and standard deviation 0.01, which makes the transition probabilities equal, $q(\psi_j,\ \psi'_j) = q(\psi'_j,\ \psi_j)$.

The conditional probability for a test value for the effect of year t, θ'_t, is

$$\pi(\theta'_t|\sigma^2, \sigma_2^2, \mu, \psi_j, D_{i,t};\ i\in R_j; j=1,...,7) = p(\theta'_t|\sigma_2^2) \prod_i p(\frac{\varepsilon_{i,t}}{D_{i,t}}|\theta'_t) \qquad (4.8)$$

with $(\theta'_t|\sigma_2^2) \sim N(0,\sigma_2^2)$ and $(\frac{\varepsilon_{i,t}}{D_{i,t}}|\theta_t) \sim N(0,\sigma^2)$. As for the region effect, a new test value is drawn from a normal distribution with mean equal to the current value and standard deviation 0.01, i.e. $q(\theta_t,\ \theta'_t) = q(\theta'_t,\ \theta_t)$.

For the variance component of the state error, the conditional probability for test value $\sigma^{2\prime}$

is

$$\pi(\sigma^{2\prime}|\mu,\psi_j,\theta_t,D_{i,t};\ i\in R_j;j=1,...,7;t=1,...,26) = \prod_i \prod_t p(\frac{\varepsilon_{i,t}}{D_{i,t}}|\sigma^{2\prime}) \qquad (4.9)$$

with $(\frac{\varepsilon_{i,t}}{D_{i,t}}|\sigma^{2\prime}) \sim N(0,\sigma^{2\prime})$. A new test value is drawn from a lognormal distribution with mean equal to the current value and standard deviation 0.1, which gives the transition probabilities $q(\sigma^2,\ \sigma^{2\prime})$ defined by a $logN(\sigma^2, 0.01)$ pdf and $q(\sigma^{2\prime},\ \sigma^2)$ by a $logN(\sigma^{2\prime}, 0.01)$ pdf. Lognormal distributions were chosen as sampling distributions for all variance components because of their long right hand tail which makes the sampling of larger values more likely and because they generate positive values.

The conditional probability for a test value for the variance component of the region effect $\sigma_1^{2\prime}$ is

$$\pi(\sigma_1^{2\prime}|\psi_j;\ j=1,...,7) = \prod_j p(\psi_j|\sigma_1^{2\prime}) \qquad (4.10)$$

with $(\psi_j|\sigma_1^{2\prime}) \sim N(0,\sigma_1^{2\prime})$. A new test value is drawn from a lognormal distribution with mean equal to the current value and standard deviation 0.1, $logN(\sigma_1^2, 0.01)$, which defines the transition probability $q(\sigma_1^2,\ \sigma_1^{2\prime})$.

The conditional probability for a test value for the variance component of the year effect $\sigma_2^{2\prime}$ is

$$\pi(\sigma_2^{2\prime}|\theta_t;\ t=1,...,26) = \prod_t p(\theta_t|\sigma_2^{2\prime}) \qquad (4.11)$$

with $(\theta_t|\sigma_2^{2\prime}) \sim N(0,\sigma_2^{2\prime})$. A new test value is drawn from a lognormal distribution with mean equal to the current value and standard deviation 0.1, $logN(\sigma_2^2, 0.01)$, which defines the transition probability $q(\sigma_2^2,\ \sigma_2^{2\prime})$.

The Markov chain which results from the conditional distributions given above is irreducible and aperiodic by design (Tierney, 1994). The burn-in period during which

all samples were discarded was 20,000 steps. Then 1377 samples were taken by keeping every 80th sample. The length of the burn-in period and the number of steps between samples were varied in some exploratory simulation runs in order to identify suitable values. The values chosen here are similar to those quoted in the literature (Craig *et al.*, 1997).

4.4 Results

4.4.1 Estimation of all parameters

The MCMC method provided a sample from the joint distribution of all parameters given the count data. Average parameter values were calculated as the average of the corresponding sample values and confidence intervals as the 2.5 and 97.5 percentiles. Average estimated red deer densities in each counting block and year are displayed together with the corresponding census count densities (Figure 4.2a & b). In years with no counts the confidence intervals were very wide. For example, the estimate of the 2.5 percentile point for block 19 in 1971 was about 10 deer per km^2 and the estimate of the 97.5 percentile point was around 80 deer per km^2 which is unbelievably high. Average deer density estimates varied dramatically from one year to the next. In some cases a fourfold increase (or decrease) in average deer densities was predicted, as for example in block 8 between 1982 and 1983.

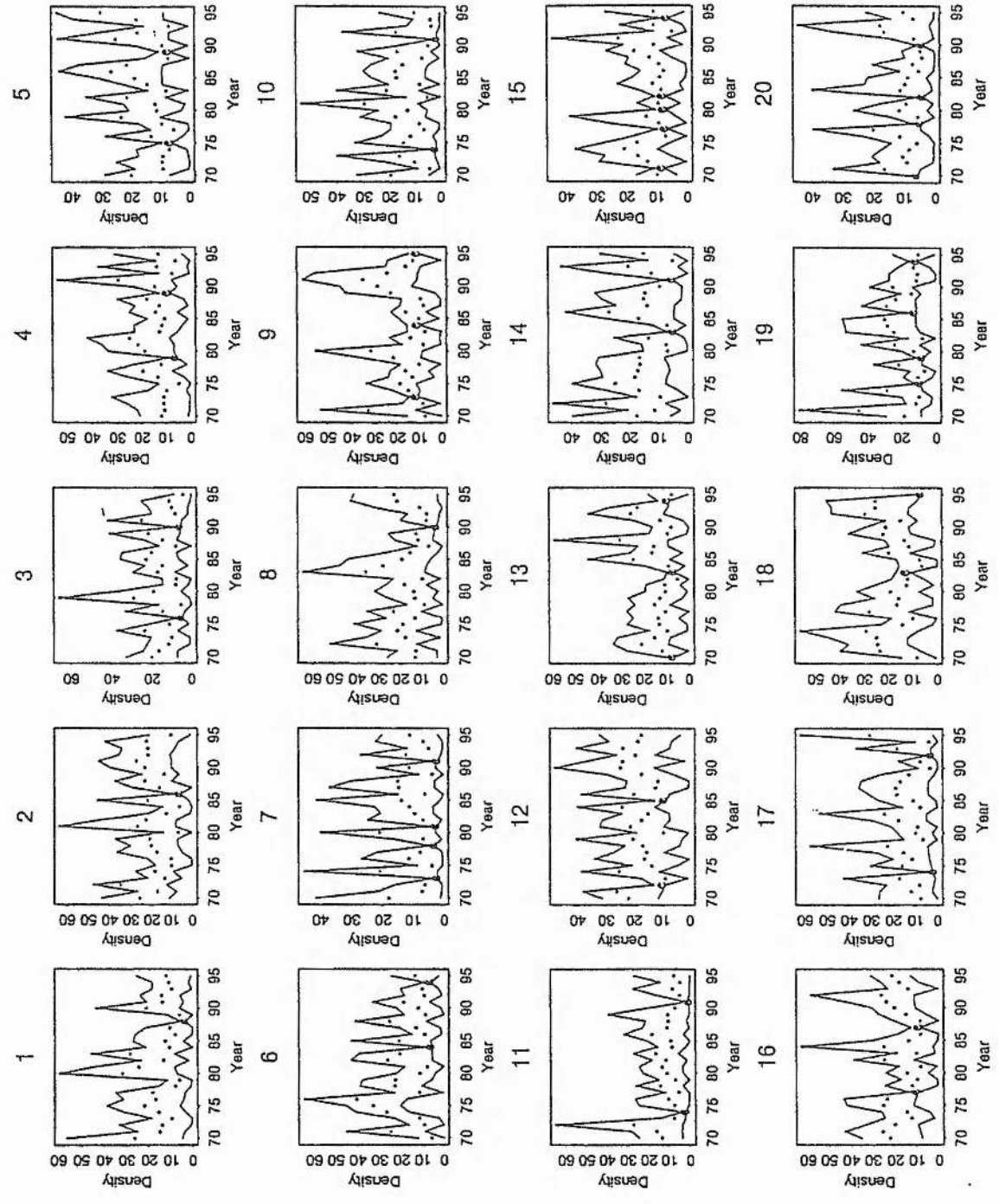


Figure 4.2a. Average estimated red deer densities per km^2 (●) and counts per km^2 (c) for counting blocks 1 to 20 from 1970 to 1995 with 95% confidence intervals for density estimates (–).

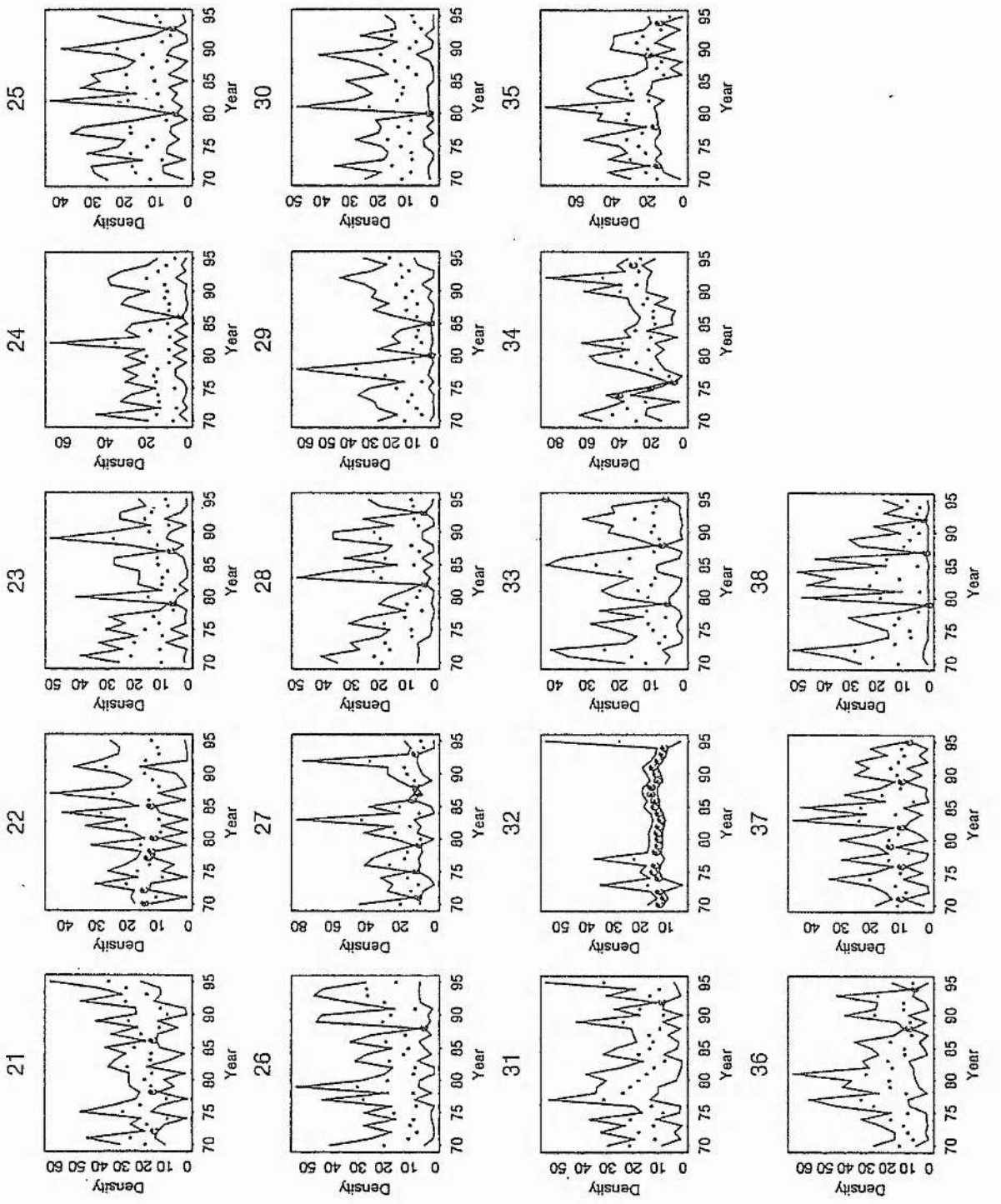


Figure 4.2b. Average estimated red deer densities per km^2 (●) and counts per km^2 (c) for counting blocks 21 to 38 from 1970 to 1995 with 95% confidence intervals for density estimates (–).

The confidence intervals for the estimated deer densities were rather large with the exception of years for which a count was available. Exploratory plots showed that this stemmed mainly from the estimate for σ^2, the variance component of the state error. From looking at the values of σ^2 at each sampling step it appeared that very high values of several thousands and occasionally much larger were obtained (Figure 4.3).

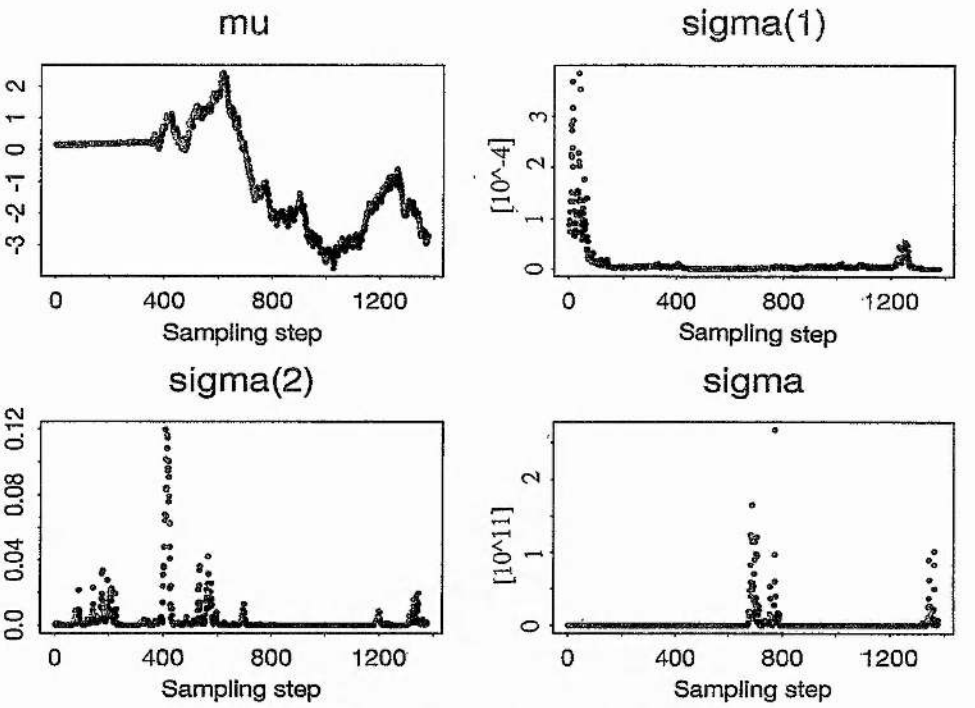


Figure 4.3. Values for selected parameters at each sampling step.

From these plots it seems that the chain had not converged for the parameters μ and σ^2 and none of the other parameters were well estimated. Hence, a modification of the estimation method seemed necessary. The options among others are changing one or several sampling distributions, introducing prior distributions for some parameters, reducing the parameter space, or updating some parameters more often than others, (e.g. keeping some parameters constant at some sampling steps or selecting randomly which parameters should be updated at a given sampling step (Gilks *et al.*, 1996)). A

change in sampling distributions was tried with little success by varying the standard deviations of sampling distributions. It was then decided to reduce the parameter space. For this reduction in the number of parameters to be estimated, the variance component σ^2 seemed to be a suitable candidate. All parameters would be estimated conditional on some constant value for σ^2 and the conditional parameter distributions used in the Gibbs sampler would then be $\pi(\Omega_m|Y^T, \Omega_{-m}, \sigma^2=const)$. As a result of fixing σ^2 the values accepted at each sampling step for the deer densities for subsequent years (same block) will be close to each other and the variance of all deer density estimates will be reduced as extreme values will not be accepted. Lacking any data on which to base the choice of a value for σ^2, a subjective reasonable choice was made and $\sigma^2=0.0016$ was assumed. This corresponds to a coefficient of variation of 4% for the state error.

4.4.2 Estimation with fixed state error

The Gibbs sampler with Metropolis-Hastings step was run conditioning on a constant value for σ^2 (=0.0016). Average (conditional) estimates for the densities of red deer in each counting block and year which were now obtained are displayed in Figures 4.4a and 4.4b. Individual blocks showed different time trends as the historic culling levels varied between blocks and over time.

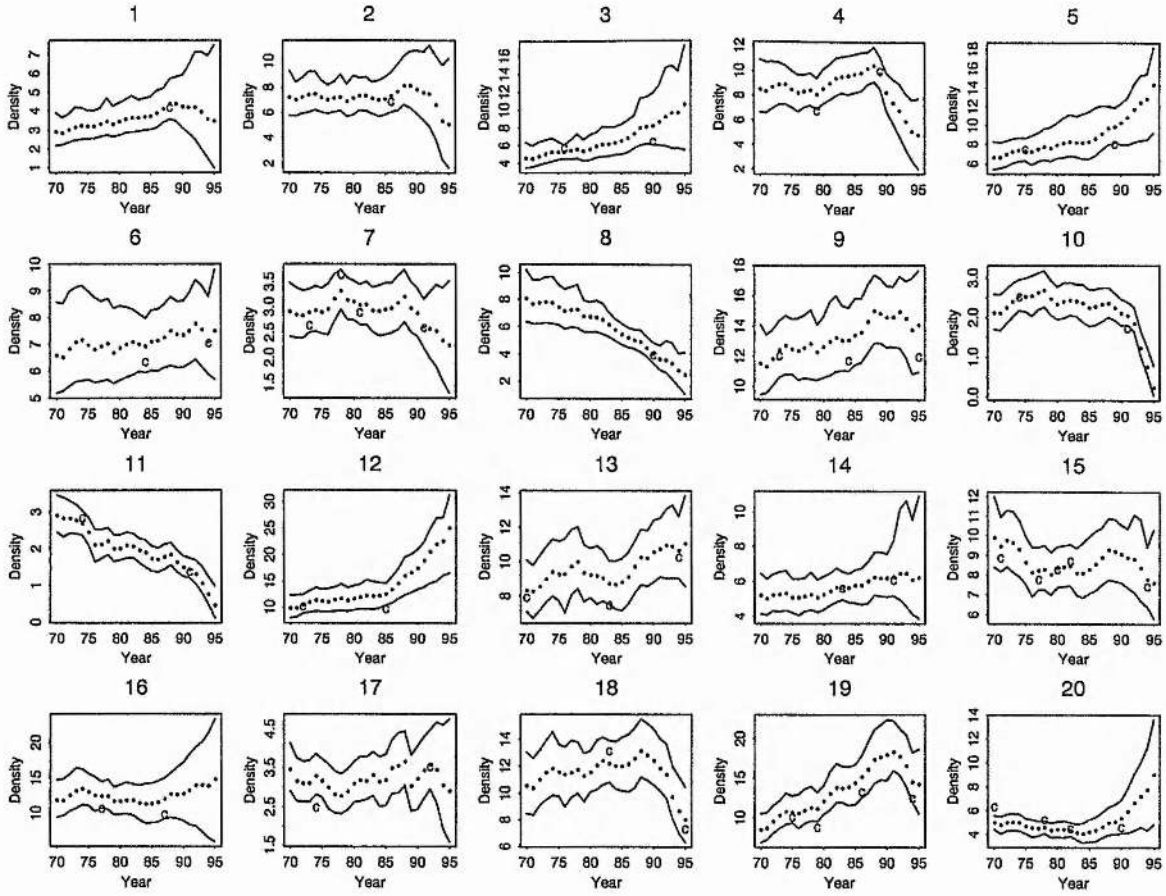


Figure 4.4a. Average estimated red deer densities per km^2 (●) and counts per km^2 (c) for counting blocks 1 to 20 from 1970 to 1995 with 95% confidence intervals for estimated densities (-) conditional on fixed state error (σ^2=0.0016).

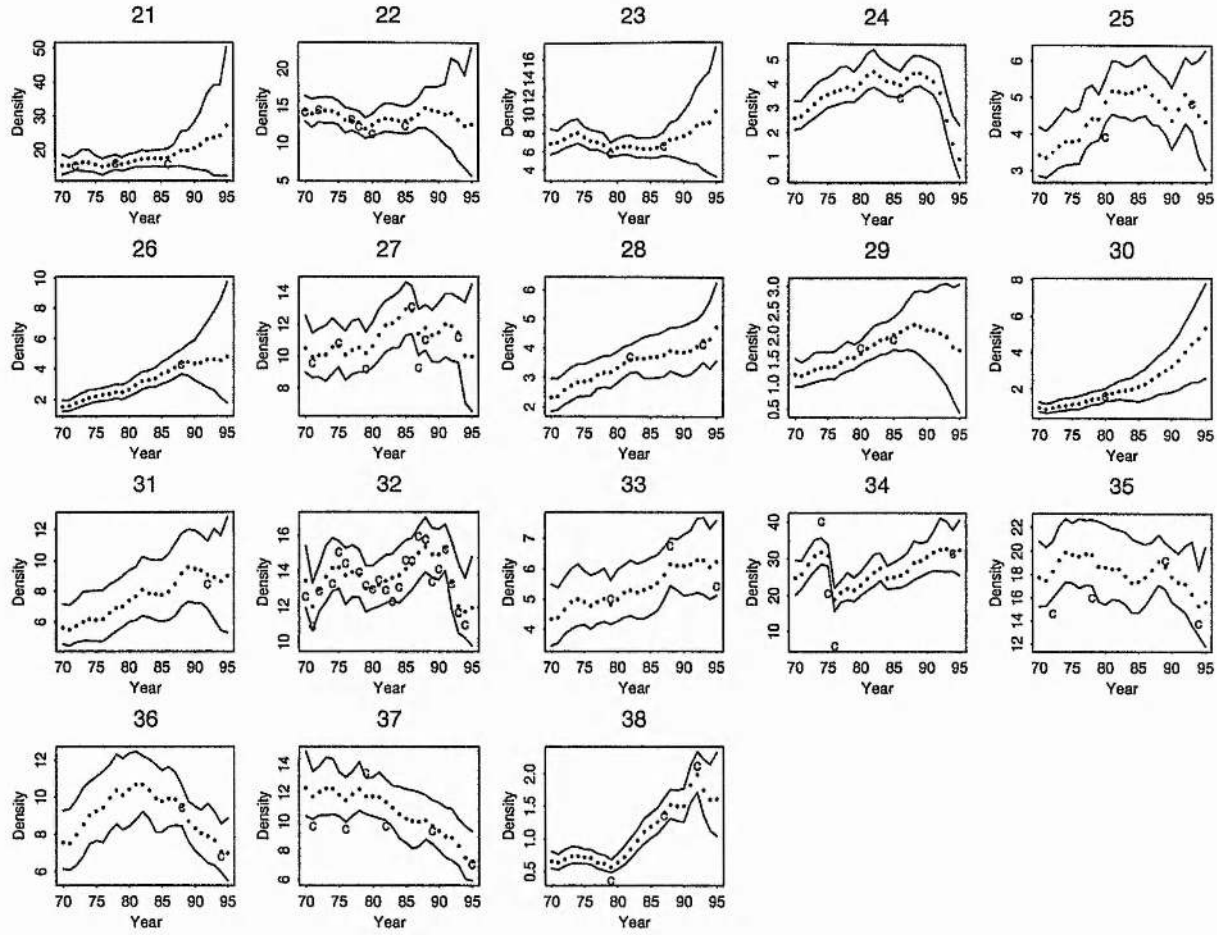
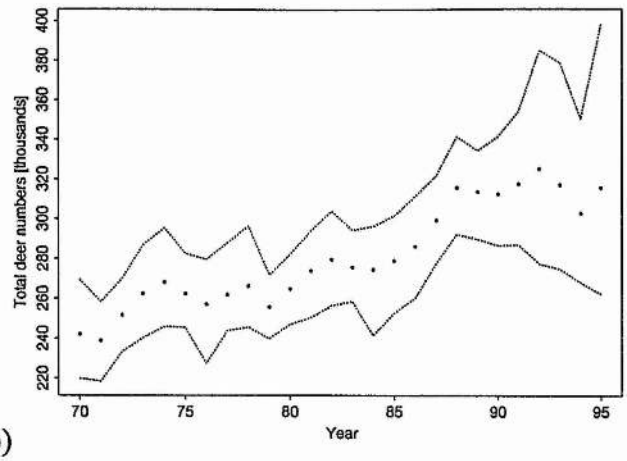


Figure 4.4b. Average estimated red deer densities per km^2 (●) and counts per km^2 (c) for counting blocks 21 to 38 from 1970 to 1995 with 95% confidence intervals for estimated densities (-) conditional on fixed state error (σ^2=0.0016).

Based on the estimates for individual blocks and years the total number of red deer in each year was estimated (Figure 4.5a). These are estimates of the total number of red deer on the open hill in the areas covered by the counting programme. The total cull over the same period is given in Figure 4.5b. The cull relates to animals shot during the autumn and winter of the year indicated whereas estimates of deer numbers are for the spring of the same year.

a)



b)

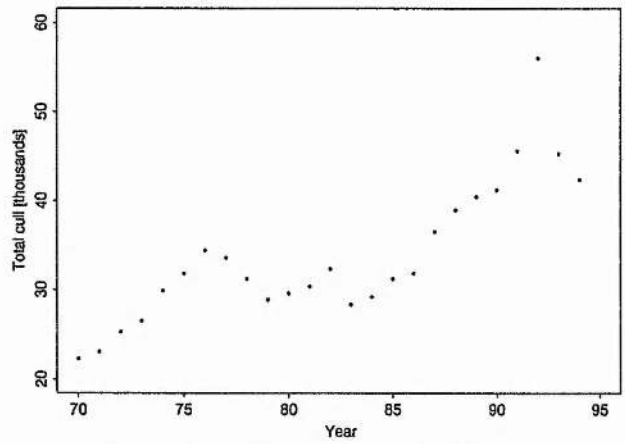


Figure 4.5 a) Average estimated total number of red deer on the open hill in Scotland from 1970 to 1995 with 95% confidence intervals conditional on fixed state error (σ^2=0.0016). b) Total cull over same period.

Deer numbers seemed to have risen over most of the period from 1970 to 1990; the precision is very poor for later years so that no clear trend emerged. Estimates of total deer numbers were compared to estimates quoted in the past by the Deer Commission for Scotland (Table 4.4). Estimates by Clutton-Brock and Albon (1989) are also given. Clutton-Brock and Albon (1989, Table A.3.1, polynomial model) estimated total deer densities between 1961 and 1986 using data from blocks that had been counted at least

twice during that period. In converting numbers to densities they excluded land not accessible to deer. However, as those area estimates were not available and to allow a rough comparison of estimated trends, their density estimates were converted into estimates of total deer numbers by multiplication with the total area of land used in the MCMC estimation (33866 km^2) and then rescaled to have the same average as the MCMC estimates for the years 1970-86. Numbers estimated by MCMC agreed rather well with the DCS estimates. The estimates by Clutton-Brock and Albon showed a 46% increase in deer numbers between 1970 and 1986 whereas the increase was 18% based on the average MCMC estimates.

Table 4.4. Total number of red deer on the open hill in Scotland. Estimates by Deer Commission (RDC, 1989), Clutton-Brock and Albon (1989)* and the MCMC method. MCMC estimates were conditional on fixed state error (σ^2=0.0016). All values were rounded to the nearest thousand.

Year	DCS estimate	Mean MCMC estimate [95% CI]	C-B & A estimates*
1963	150,000	-	221,000
1969	180,000 - 185,000	-	216,000
1970	-	242,000 [220,000 - 269,000]	229,000
1974	200,000	268,000 [246,000 - 296,000]	268,000
1977	270,000	262,000 [244,000 - 288,000]	268,000
1979	255,000	256,000 [240,000 - 272,000]	258,000
1986	290,000	286,000 [260,000 - 311,000]	335,000
1989	300,000	313,000 [290,000 - 334,000]	-
1995	-	316,000 [262,000 - 399,000]	-

*Estimates by Clutton-Brock and Albon were obtained by multiplying estimates of total deer densities (polynomial model) with the total area covered by the MCMC method (33866 km^2) and then rescaling them to have the same mean for the years 1970-86 as the MCMC estimates.

Average estimated region effects ψ_j with 95% confidence intervals are displayed in Figure 4.6. Positive region effects for the net population change rate were found for regions 6 and 4, which contain the counting blocks in the south west and east respectively. All other regions had negative region effects for the net population change rate. Hence, on average regions 4 and 6 had larger net population change rates than the remaining regions.

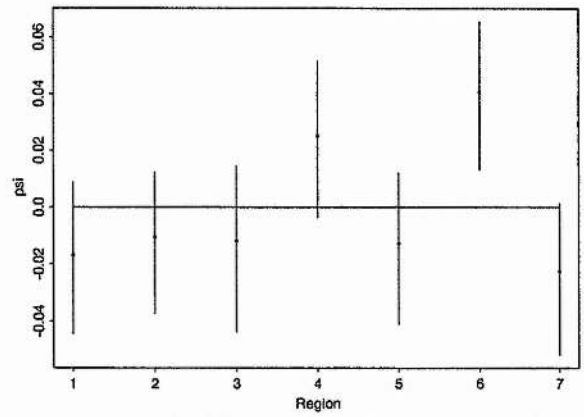


Figure 4.6. Average estimated region effects ψ_j with 95% confidence intervals conditional on fixed state error (σ^2=0.0016).

Average estimated time effects θ_t showed no trend over time and the 95% confidence intervals were rather wide (Figure 4.7).

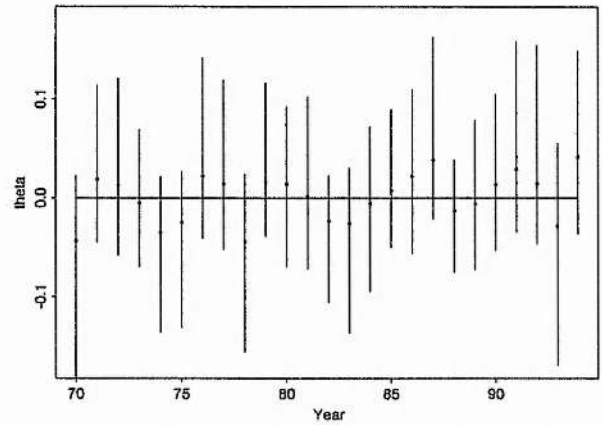


Figure 4.7. Average estimated time effects θ_t from 1970 to 1994 with 95% confidence intervals conditional on fixed state error (σ^2=0.0016).

To assess whether the Markov chain had been run long enough, rejection rates of test values were monitored. The rejection rates seemed to be constant over the sampling period for most parameters. Figure 4.8 shows rejection rates for selected parameters calculated over the sampling steps between the samples that were taken, that is for the 79 samples that were not stored.

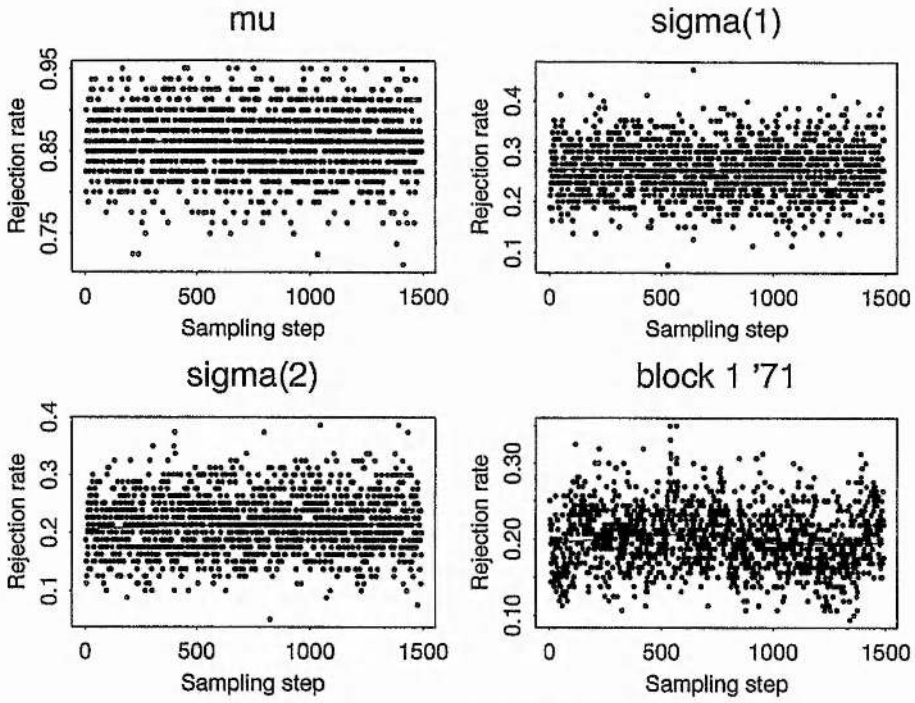


Figure 4.8. Rejection rates during sampling period for selected parameters. Estimation conditional on fixed state error (σ^2=0.0016).

For assessing convergence, the value for the total number of red deer in 1995 at each sampling step was calculated by summing individual block values. These values were then plotted against the sampling step (Figure 4.9). The values increased for most sampling steps in the direction of step 1 to step 1500 which seemed to indicate that the chain might not have converged, at least not for parameters which represent red deer densities in 1995.

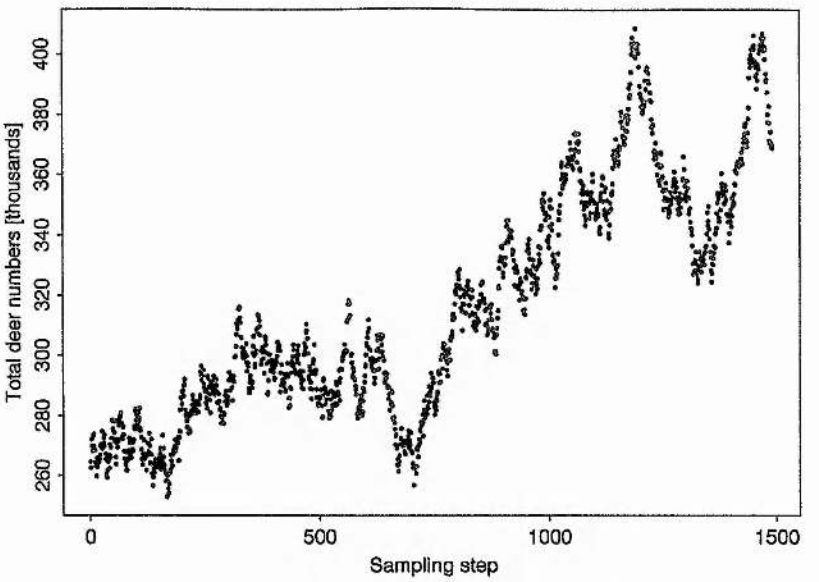


Figure 4.9. Total number of red deer in 1995 at each sampling step. Estimation conditional on fixed state error (σ^2=0.0016).

Values for some of the other parameters showed less pronounced trends but high autocorrelations when plotted against the sampling step (Figure 4.10).

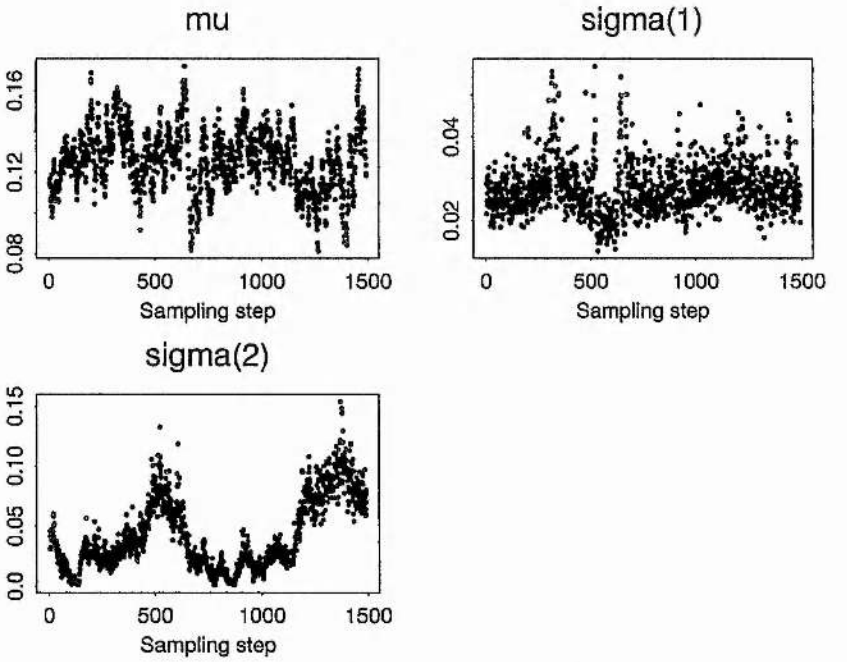


Figure 4.10. Values for selected parameters at each sampling step. Estimation conditional on fixed state error (σ^2=0.0016).

Correlations between parameter values retained at subsequent sampling steps of the Markov chain were calculated. These autocorrelations were high up to a lag of six for most parameters (Figure 4.11). This means that most variance estimates will be too small. However, if required, the bias in variance estimates due to autocorrelation could be corrected for.

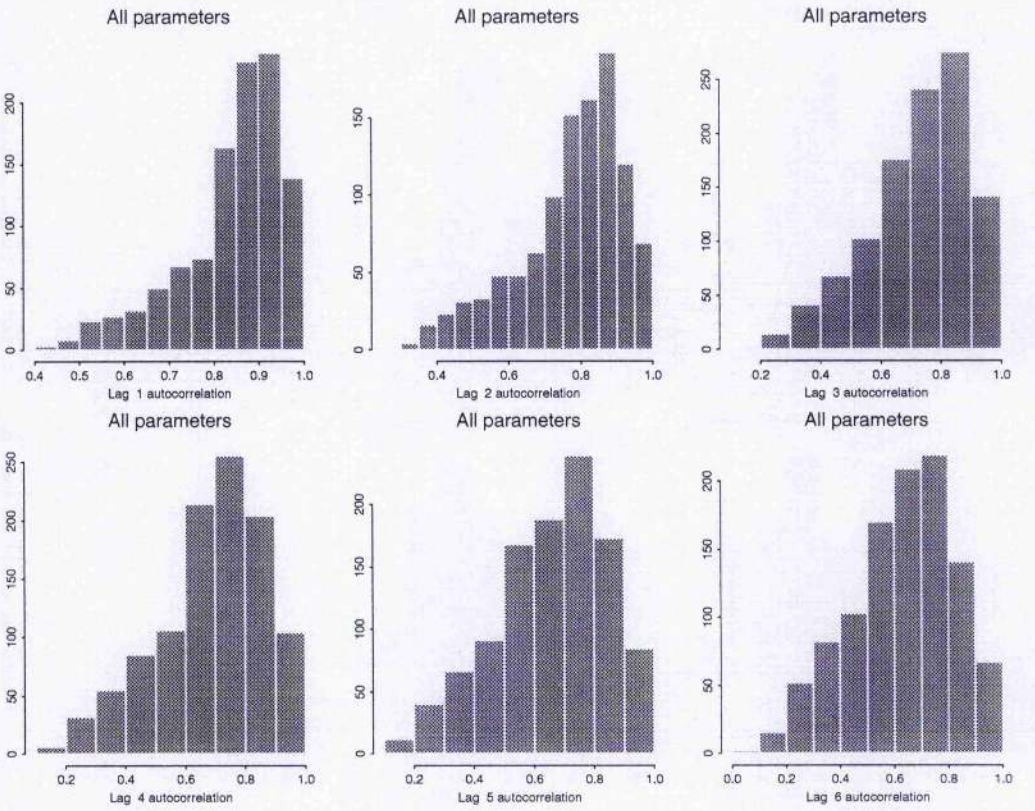


Figure 4.11. Histogram for all parameters of lag-1 to lag-6 autocorrelations for adjacent samples taken during the sampling process.

These plots indicated that although fixing the state error seemed to have improved the estimation process, doubts remained about the results. In particular, convergence of the Markov chain might still not have been achieved.

4.5 Counting frequency

It might be of interest to know how often individual blocks would have to be counted in order to estimate total deer numbers with minimum variance when annual counting effort is restricted. Suitable weather and the size of the counting team available would usually restrict the effort that can be put into counting.

A simple approach for estimating how often blocks should be counted, which is independent of the MCMC method used above, would be to assume that the number of deer in each block is fixed and that we are dealing with a problem of optimal resource allocation in stratified random sampling. Here the blocks would be regarded as strata with sampling units extending over time. The theory for optimum resource allocation in stratified random sampling with limited resources can be applied to this problem (Cochran, 1953; p. 75). In this case, the frequency f_i at which an individual block i has to be counted is given by

$$f_i = \frac{1}{B} \left(\sum_i S_i/\sqrt{e_i}\right) / \left(S_i/\sqrt{e_i}\right) \quad \text{and} \quad B = E \left(\sum_i S_i/\sqrt{e_i} \right) / \left(\sum_i S_i\sqrt{e_i} \right) \qquad (4.12)$$

where B is the average number of blocks counted per year; E is the total allowable effort per year. Denote the effort required to count block i by e_i, and the standard deviation of an estimate of the population size in that block by S_i.

It is assumed that the standard deviation of a population estimate is proportional to the number of deer counted, which implies a constant coefficient of variation for the counting error, an assumption which has been made before (section 4.2). The average of the DCS counts for each block was used to estimate S_i. The effort required to count

a block is expressed as the number of person-days required to count it (Table 4.5). Counting effort is not directly related to the number of deer in a block as other factors play a role in how long it takes to count a block. The total allowable effort per year is assumed to be 400 person-days which usually would mean a team of ten DCS counters working for 40 days and corresponds to the counting effort of the Deer Commission in recent years. Based on these assumptions and equations (4.12) it was calculated how often each counting block should be counted in order to minimize the variance of the estimate of total deer numbers (Table 4.5).

Table 4.5. Number of person-days (number of days for a counting team of 10 persons) needed to count a block (DCS pers. comm.) and frequency in years at which blocks should be counted to reduce variance of estimate of total deer numbers.

Block	Effort [person days]	Counting frequency [years]	Block	Effort [person days]	Counting frequency [years]
1	50	4	20	100	6
2	60	5	21	50	4
3	100	7	22	40	7
4	100	6	23	60	6
5	100	7	24	30	9
6	120	6	25	30	16
7	30	26	26	40	12
8	40	14	27	20	6
9	60	2	28	40	15
10	30	38	29	10	44
11	20	64	30	50	47
12	150	4	31	10	87
13	30	16	32	20	18
14	20	6	33	80	11
15	40	10	34	3	31
16	120	3	35	40	6
17	30	20	36	20	5
18	200	3	37	20	12
19	150	3	38	10	19

In order to reduce the variance of the estimate of the total number of red deer in all counted blocks, the required counting frequency for some blocks is very low, for example 87 years for block 31. This means that block 31 (with a recorded population size of 1451 in 1994) is not contributing many deer to the total number and therefore a new count is not required frequently. In practice, counting some blocks only every 87 or even every 20 years would not be acceptable. One might want to impose say ten years as the maximum time between subsequent counts. An additional constraint for a practical counting scheme might also be the continuation of the annual counts on Rum (block 32). A possible counting scheme based on the results of table 4.5 and taking those additional constraints into account is presented in table 4.6. In order to count each block at least once during the ten year period, the allowable counting effort per year was increased to a maximum of 470 person days per year.

Table 4.6. Counting scheme for reducing variance of estimates of total deer numbers conditional on counting each block at least once during the ten year period.

Year	Block numbers	Total effort [person days]
1	1, 6, 12, 21, 32	450
2	2, 3, 14, 16, 23, 32, 35, 36	440
3	18, 19, 29, 32	470
4	4, 7, 8, 9, 13, 15, 22, 27, 29, 32, 34, 37, 38	423
5	1, 12, 16, 17, 21, 32	420
6	5, 9, 10, 18, 24, 32	440
7	2, 6, 19, 25, 32, 35, 36	440
8	9, 11, 14, 16, 23, 26, 28, 30, 31, 32	440
9	1, 3, 4, 20, 21, 27, 32	450
10	12, 18, 21, 27, 32	440

The calculations presented here are simplistic and therefore only intended as guidelines. More sophisticated studies would be needed to find the best counting scheme when total deer numbers are estimated by Markov chain Monte Carlo methods.

4.6 Discussion

Initial attempts to use the Kalman filter for the estimation of deer numbers per counting block had failed. For the model tried, the algorithm did not converge and results depended very much on starting conditions. The Markov chain Monte Carlo method which was then used was easily adapted to different model assumptions although it was far more computer intensive. However, the parameter estimation using Markov chain Monte Carlo methods was not completely successful. By assuming a constant coefficient of variation for the state error, plausible results were obtained though probably without reaching convergence. The agreement between estimated deer numbers and counts varied widely between blocks. In some blocks deer estimates appeared to be reasonable whereas in others, counts were quite different from the average estimates. This might indicate that in those blocks, the coefficient of variation of the state error or the counting error or both were larger than the assumed 4% and 10% respectively. A large variation in the state error can have several causes. Underreporting of the number of culled animals would lead to a larger state error when one might expect otherwise. This underreporting could vary between counting blocks. Movement of animals between blocks would also increase the state error. No information was available on the magnitude of the state error. Hence, the selected 4% coefficient of variation was somewhat arbitrary.

It is expected that more count data, especially for blocks which had only one or two counts, would improve parameter estimation and in particular would lead to better estimates of region effects. The counts made by Deer Management Groups themselves might offer a possibility to augment the data set.

A different line of investigation could look at the possibilities for improving the estimation process via MCMC methods by increasing the rate of convergence. For example, introducing informative prior distributions or sampling directly from the full conditional parameter distributions of some (or all) parameters which amounts to a Gibbs sampler without the Metropolis-Hasting steps could be tried. Various ways for improving sampling distributions have been proposed (Gilks *et al.*, 1995) and might be tested.

An alternative route for obtaining better estimates of total deer numbers would be to improve the counting scheme. In section 4.5 this question was approached from an angle of optimal resource allocation. It was assumed that it was of interest to obtain counts of individual counting blocks as well as estimates of total red deer numbers in Scotland. A counting scheme based on a ten year counting period was presented.

If however estimates of total deer numbers are the main interest and counts for individual counting blocks are provided by other interested parties, for example Deer Management Groups, a different route could be taken. For the purpose of monitoring total red deer numbers, Scotland could be divided into three to five regions which could include areas which have never been censused. For practical reasons, the boundaries of these regions should follow current DMG boundaries and each region would contain

a number of DMGs. For example, the seven regions used for analysis of the questionnaire survey data in chapter 2 (Figure 2.1) could be used as a starting point; regions 1 and 2 and 3, 4 and 5 could be combined to obtain four larger regions. Deer numbers within each region would be estimated by aerial line transect surveys (chapter 3) and repeated on a regular cycle. Aerial line transect surveys have the advantage of providing estimates for the precision of abundance estimates and for large areas are generally faster and cheaper than census counts (section 3.4). Given sufficient resources, each region would be surveyed every year. A simplistic calculation can be made to obtain the expected coefficient of variation of an overall abundance estimate. Assuming 400 person-days are available per year, this gives 80 survey days with teams of five persons. A rough calculation based on the questionnaire returns (chapter 2) gives an overall deer density of 10.5 deer per km^2 in Scotland. Assuming transect lines with an overall length of 200 km can be surveyed in a day and making the same assumptions about mean group size, effective search half-width and so on as for the case study in section 3.4, it is expected that the coefficient of variation of the overall deer abundance estimate would be about 19%.

If not enough resources are available to cover all regions every year, or a more precise abundance estimate is desired, at least one region would be surveyed per year which means each region would be surveyed at least every 3-5 years depending on the number of regions. Abundance estimates could then be used to monitor red deer numbers on a national scale and also provide management support on a regional level. Following this scheme would reduce the need for statistical modelling and restrictive model assumptions and would even make them redundant if all regions were surveyed every year.

For efficient management of red deer in Scotland, national figures are less important and individual populations become the focus of interest. A management model for an individual red deer population will be the topic of the next chapter.

Chapter 5 Management model for red deer populations

5.1 Introduction

In the previous chapter red deer numbers on a Scotland wide scale were considered. In this chapter, the management of an individual population is looked at. Management strategies for various red deer populations in Scotland have been explored in the past using population dynamics models (e.g., Beddington, 1974; Clutton-Brock and Lonergan, 1994; Buckland *et al.*, 1996). However, these investigations have been carried out for particular populations and are not readily transferable to populations experiencing different environmental conditions. A common approach in that case is to estimate model parameters using data from well studied populations. The relevance of these estimates to other similar populations is then assessed by examining the sensitivity of outputs to systematic variation in the input parameters about their point estimates. This strategy can be improved when some local information is available by using this information to calibrate the model for local conditions as has been done for water catchment models (Beven and Binley, 1992). Beven and Binley attached weights to a selection of plausible model parameters. These weights were calculated using a goodness-of-fit function which compared model predictions with local observations and were then used to weight future predictions.

Few attempts have been made to tackle the problem of calibrating population dynamics models and including parameter uncertainty in management models within the framework of statistical inference. A sophisticated approach based on ideas of Bayesian estimation has been developed by Raftery *et al.* (1995) for deterministic population

dynamics models for the case when the information available for estimation comes from various sources including expert knowledge. A problem of that approach which arises from Borel's paradox (Wolpert, 1995) will be discussed later.

For many red deer populations in Scotland local data are available as time series of census counts and the number of animals shot annually (chapter 2). Commonly, red deer counts are classified as stags, hinds and calves. Culled animals are recorded in the same categories although, increasingly, shot animals are aged.

The state space approach offers a natural way of linking models for the number of animals in each category with models for the observations where the observations are subject to some random error. The state space model formulation has already been used in chapter 4 for modelling deer densities with a simple linear model. A more complex age and sex structured population dynamics model is required now in order to be able to explore a range of management options for an individual red deer population. Such a population dynamics model is most likely nonlinear. Hence, the classical Kalman filter which could be used for the simple model, though with little success, cannot be applied for obtaining parameter estimates of the complex model. Extensions of the Kalman filter to non-Gaussian and non-linear models have been proposed (Kitagawa, 1987; Meinhold and Singpurwalla, 1989; Fahrmeier, 1992; Naik-Nimbalkar and Rajashi, 1995). However, the applicability of those extensions often depends on the assumed error distributions and the particular model formulation. The Kalman filter method has been used successfully for estimating fish populations using a linear approximation to a non-linear population dynamics model (Gudmundsson, 1994).

Bayesian estimation offers a unified approach to parameter estimation for linear and non-linear models and for any type of error distribution (e.g., Robert, 1992). Bayesian estimation is based on combining prior information on parameters of interest with observations and provides the joint posterior parameter distribution. If applied to time series observations, posterior parameter distributions at one time point become prior distributions for the following estimation step. The classical Kalman filter can be regarded as a special case of sequential Bayesian estimation of time series (Meinhold and Singpurwalla, 1983).

The sequential Bayesian approach seems well suited for the problem of calibrating a population dynamics model for red deer which has been parameterised initially for some particular population(s). All model parameters and the initial age and sex structure of the population are given prior distributions and the joint posterior distribution is obtained at each time step. One advantage of the sequential updating procedure is that each time new local data become available, for example when a census is carried out, parameter values can be updated and new management decisions taken. Such an adaptive approach was proposed by Johnson *et al.* (1997) for waterfowl management.

The complications of Bayesian estimation are often due to complex integration problems for non conjugate parameter distributions. Many methods have been developed in recent years that exploit increased computing power to simulate samples from posterior distributions (e.g., Gelfand and Smith, 1990; Besag and Green, 1993; Newton and Raftery, 1994). Smith and Gelfand (1992) suggested Bayesian parameter estimation by sampling-resampling. The sampling/importance resampling algorithm (SIR) (Rubin, 1988) is often used to obtain a sample from the joint posterior

distribution (e.g. McAllister *et al.*, 1994; Raftery *et al.*, 1995). In the SIR algorithm, a large number (typically hundreds of thousands) of initial samples are drawn from the prior distribution from which a smaller sample is then selected proportional to some likelihood weights. Rubin (1988) showed that the selected values are a good approximation to a sample from the required joint posterior distribution if the first sample is much larger than the second.

The main motivation for calibrating the population dynamics model for red deer is to obtain a set of parameter values that gives good predictions for the population of interest. As the local data for red deer are sparse and aggregated and the population dynamics model contains a large number of parameters, many of these parameters will be confounded and marginal parameter estimates will not be meaningful. Robustness and speed are two important issues if the calibration method and the calibrated population dynamics model are going to be used by deer managers themselves to explore management options. Hence, instead of the SIR algorithm, the use of a smoothed weighted bootstrap of posterior model parameter values is proposed to reduce the required number of samples. In a smoothed bootstrap, a random sample is drawn from the kernel density estimate of the distribution (Silverman, 1986). West (1992) has used kernel density estimation to approximate prior and posterior parameter distributions. Posterior estimates of the population numbers are improved by a linear filtering step.

5.2 Model

The model and the accompanying updating algorithm are written using the state space formulation. Birth and death processes, ageing and culling change the numbers and age distribution of red deer populations. These processes are included in the population dynamics model for which the convenient formulation

$$\boldsymbol{n}_t = \boldsymbol{M}(\boldsymbol{b})\ \boldsymbol{n}_{t-1} - \boldsymbol{c}_{t-1} + \boldsymbol{e}_t \qquad (5.1)$$

is used. $\boldsymbol{n}_t$ is a vector of length r whose ith element $n_{i,t}$ denotes the number of animals in the ith age-sex class in year t. The vector of culled animals, $\boldsymbol{c}_{t-1}$, has length r and is assumed to be known, though culls might be aggregated across age classes. $\boldsymbol{M}(\boldsymbol{b})$ is an $r \times r$ transition matrix whose elements represent survival and recruitment rates which in turn are functions of the model parameter vector $\boldsymbol{b}$; $\boldsymbol{e}_t$ are departures from expectation which are carried forward into future populations. These departures from expectation are due to the stochastic nature of survival and recruitment. $\boldsymbol{M}(\boldsymbol{b})$ is formulated in a way to reduce parameter correlations (Ross, 1990). The formulation of the population dynamics model (5.1) is general and the actual chronological order of natural mortality, birth and culling has to be taken account of in any application. A modified version of (5.1) will be used in section 5.5 when the algorithm is applied to red deer. However, the proposed formulation is convenient for expressing the basic ideas of the updating algorithm.

The observation equation describes the relationship between the number of animals in each age-sex class and the observed counts

$$\boldsymbol{y}_t = \boldsymbol{A}\ \boldsymbol{n}_t + \boldsymbol{w}_t \qquad (5.2)$$

where $\boldsymbol{y}_t$ is the count vector of length s, $\boldsymbol{A}$ is a known $s \times r$ matrix mapping the r age-

sex classes into s ($s<r$) classes used for counts and w_t is the counting error. In the case of red deer, counts are aggregated as stags, hinds and calves, thus s=3, whereas r is 40 (taking age classes 1-13 for hinds without calf and stags and classes 2-13 for hinds with calf, and two additional classes for male and female calves).

5.3 Updating algorithm

The overall framework of the proposed updating algorithm is Bayesian with prior distributions for all model parameters $\boldsymbol{b}$ and population numbers $\boldsymbol{n}_1$ at t=1 in (5.1). Calculations are carried out by simulation as in Gelfand and Smith (1990). Stepping through the time series of observations year by year gives samples from the joint posterior parameter distributions at time t=2,3,.... Before proceeding with the description of the algorithm, some notation needs to be defined. The vector of simulated values of the model parameters $\boldsymbol{b}$ in (5.1) using information up to and including time t is referred to as simulated parameter values $\beta_{j,t}$, j=1,...k, where k such simulated parameter vectors have been created. For the number of animals $\boldsymbol{n}_t$ at time t in (5.1), the vector of simulated deer numbers $\nu_{j,t}$, j=1,...k, is generated. Together the simulated parameter values and simulated deer numbers form simulation set $\Psi_t = \{\psi_{j,t}=(\beta_{j,t}, \nu_{j,t}); j=1,...k\}$; $\psi_{j,t}$ is a simulation set member. The vector of expected simulated counts at time t is denoted as $\gamma_{j,t} = A\nu_{j,t}$, j=1,...$k$. Observed counts are $\boldsymbol{x}_t$ and the last count took place in year T.

All model parameters are assigned independent prior distributions based on detailed population studies. Prior distributions for the initial deer numbers are derived from the counts at time t=1 and some assumptions about relative frequencies of different age

groups (see Section 5.5.2 for details). The steps of the updating algorithm are as follows (Figure 5.1).

At the initialisation step, for each member of the simulation set independent random samples are drawn from the prior distributions of model parameters and initial deer numbers are created. This gives the simulation set $\Psi_1 = \{(\beta_{j,1}, \nu_{j,1}); j=1,...k\}$.

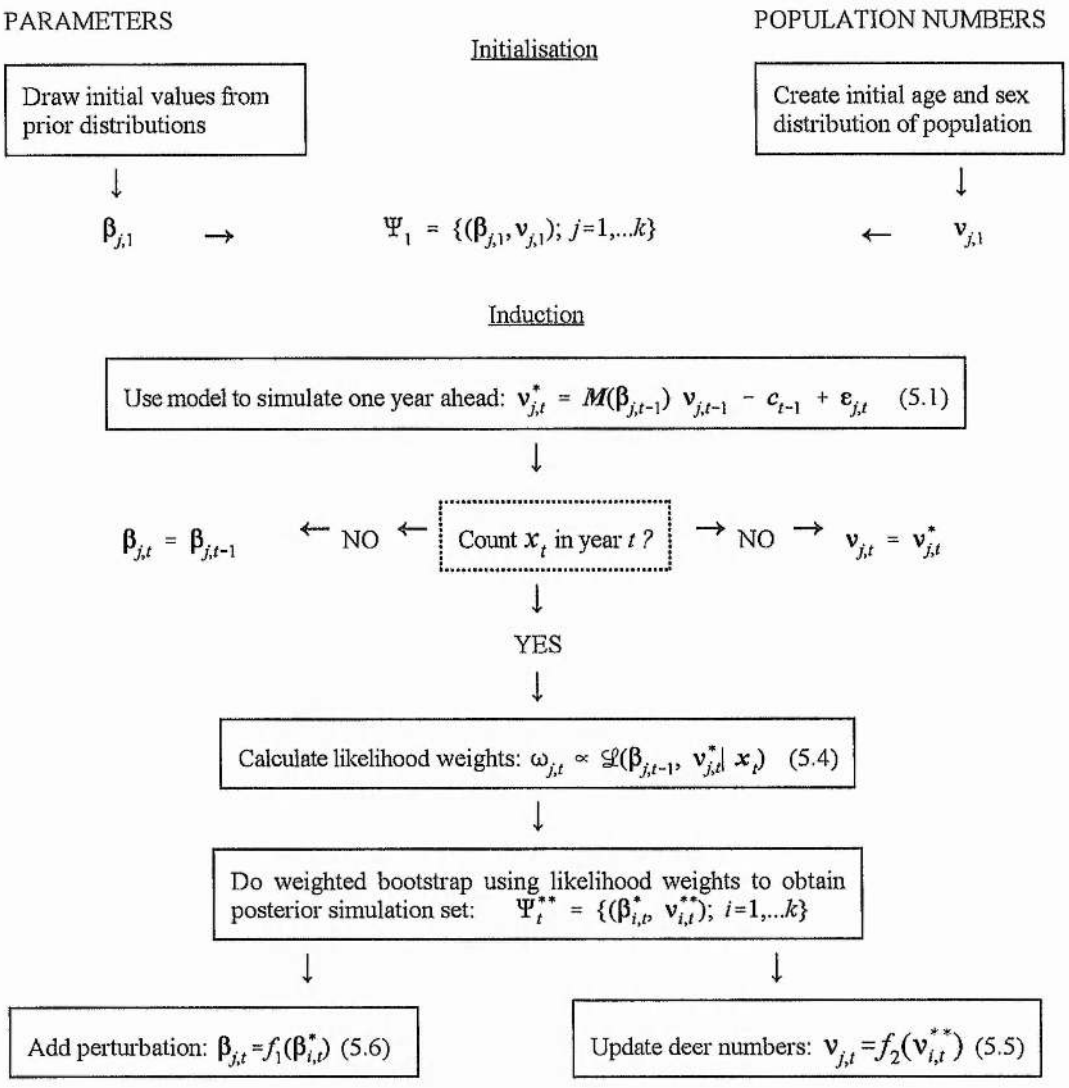


Figure 5.1. Schematic view of the updating algorithm for calibrating population dynamics model. Numbers refer to equations in the text.

In subsequent steps, for t=2,...T, the population dynamics model is used for all simulation set members to map the simulated deer numbers in year t-1, $\nu_{j,t-1}$, to the simulated deer numbers in year t, $\nu^*_{j,t} = M(\beta_{j,t-1})\ \nu_{j,t-1} - c_{t-1} + \varepsilon_{j,t}$; the simulation variation $\varepsilon_{j,t}$ is the result of binomial draws for the number of animals surviving in each age-sex class and the number of animals born to mothers in different age and reproductive categories. Predictions of deer numbers at time t, which will be referred to as one year ahead predictions, are estimated by the average of all simulation set members; the prediction variance is estimated by the variance of the simulation set. Confidence intervals for one year ahead predictions are obtained by the percentile method. One of two routes is pursued now, depending on whether a count is available for year t or not.

No count for year t

If no count is available for year t, the simulated parameter values $\beta_{j,t-1}$, stay unchanged and become the parameter values for simulating the next year; hence $\beta_{j,t} = \beta_{j,t-1}$. The simulated deer numbers for year t, $\nu^*_{j,t}$, are used directly for the next time step and $\nu_{j,t} = \nu^*_{j,t}$.

Count for year t

If a count is available for year t, the likelihood value for each simulation set member $\psi^*_{j,t} = (\beta_{j,t}, \nu^*_{j,t})$ given the count x_t in year t and the simulated numbers in year t-1 is calculated

$$\mathcal{L}(\beta_{j,t-1}, \nu^*_{j,t} | x_t, \nu_{j,t-1}) = p(x_t | \beta_{j,t-1}, \nu^*_{j,t}, \nu_{j,t-1}) \qquad t>1 \qquad (5.3)$$

The conditional distribution of counts is multinomial strictly speaking. However, for

large populations the normal distribution provides a good approximation. Thus, the conditional distribution of the observations in (5.2) is

$$(y_t|n_t,\ b_t,\ n_{t-1}) \sim MVN(An_t,\ A\Sigma^{e_t}A' + \Sigma^{w_t})$$

This gives likelihood weights $\omega_{j,t}$

$$\omega_{j,t} = \frac{\exp(-\frac{1}{2}(x_t - A\nu^*_{j,t})'\ (\hat{\Sigma}^{y_t})^{-1}\ (x_t - A\nu^*_{j,t}))}{\sum_j \exp(-\frac{1}{2}(x_t - A\nu^*_{j,t})'(\hat{\Sigma}^{y_t})^{-1}(x_t - A\nu^*_{j,t}))} \tag{5.4}$$

$\hat{\Sigma}^{y_t}$ is an estimate for the variance-covariance matrix of counts and has two components. The first component is the variance-covariance Σ^{e_t} of deer numbers and the second component is the variance-covariance of the counting error. It is suggested to estimate Σ^{e_t} from the simulation set as $\mathrm{Cov}(\nu^*_{1,t},\ldots,\nu^*_{k,t})$ and obtain an empirical estimate for the covariance of the counting error. The variance-covariance matrix of the predicted counts is then estimated by $\hat{\Sigma}^{y_t} = A\ \hat{\Sigma}^{e_t}\ A' + \hat{\Sigma}^{w_t}$.

A weighted bootstrap of the simulation set $\Psi^*_t = \{(\beta_{j,t-1}, \nu^*_{j,t});\ j=1,\ldots k\}$ using likelihood weights $\{\omega_{j,t};\ j=1,\ldots k\}$ yields the posterior simulation set $\Psi^{**}_t = \{(\beta^*_{i,t}, \nu^{**}_{i,t});\ i=1,\ldots k\}$ which is a sample from the joint posterior distribution (Smith and Gelfand, 1992). Many of the simulated parameter values $\beta^*_{i,t}$ in the posterior simulation set will be identical if some of the simulated parameter values $\beta_{j,t-1}$ have large likelihood weights $\omega_{j,t}$ and are therefore selected several times in the weighted bootstrap. Hence, to improve the coverage of the parameter space by the simulated parameter values the parameter values in the posterior simulation set are smoothed (Silverman, 1986). Simulated deer numbers are updated in order to reduce the systematic departure of simulated counts from observed counts while allowing for random departures due to counting error.

The updating of simulated deer numbers in each member of the posterior simulation set, $(\beta^*_{i,t}, \nu^{**}_{i,t})$, is similar to the linear filtering of the Kalman filter. It brings the simulated counts at time t closer to the observed counts

$$\nu_{j,t} = \nu^{**}_{i,t} + B \{A \hat{\Sigma}^{e}_{t} A' [\hat{\Sigma}^{y}_{t}]^{-1} (x_t - A\nu^{**}_{i,t})\} \quad j=1,..k;\ i=1,...k. \qquad (5.5)$$

Matrix $\boldsymbol{B}$ is of rank r x s and translates the changes of stags, hinds and calves given by $\{\cdot\}$ into changes of individual age-sex classes by retaining the relative proportions of age classes in $\nu^{**}_{i,t}$.

In the smoothed bootstrap of model parameters, a random perturbation ϵ_t drawn from a kernel function is added to each element of each vector of simulated parameter values $\beta^*_{i,t}$ in the posterior simulation set to give vectors of smoothed simulated parameter values at time t

$$\beta_{j,t} = \bar{\beta}^*_{.t} + h\,(\beta^*_{i,t} - \bar{\beta}^*_{.t}) + \epsilon_{j,t}\,(1 - h^2)^{1/2} \quad j=1,...k;\ i=1,...k;\quad 0 \le h \le 1 \qquad (5.6)$$

$$\epsilon_{j,t} \sim MVN(0,\ Cov(\beta^*_{j,t}))$$

where $\bar{\beta}^*_{.t} = \sum_{j=1}^{k} (\beta_{j,t-1}\ \omega_{j,t})$ is the weighted average of all simulated parameter values at time *t-1* and $Cov(\beta^*_{j,t})$ is the corresponding variance-covariance matrix. Performing the calculations in this way rather than using the posterior simulation set reduces the sampling variance in $\bar{\beta}^*_{.t}$. The mean and variance of the joint posterior parameter distribution are preserved in this formulation of the smoothed bootstrap but third and higher order moments are not. h is the smoothing factor. If h is chosen to be 1, no smoothing of posterior simulated parameter values is carried out; if h is 0, this is equivalent to a parametric bootstrap, in which the joint posterior parameter distribution is assumed to be multivariate normal and is treated as if it was independent of the posterior distribution of deer numbers. New parameter values are generated from this

multivariate normal distribution with mean $\bar{\beta}^*_{.t}$ and variance-covariance matrix $Cov(\beta^*_{j,t})$. For intermediate values h acts as a smoothing factor.

The best choice for the smoothing factor depends on a number of considerations. Although the mean and the variance of the posterior parameter distribution at time t are preserved for any choice of smoothing factor h, the prediction variance for deer numbers at time t+1 estimated from the simulation set variance depends on the value of h. If h=1, a number of simulation set members will have identical vectors of simulated parameter values as well as identical deer numbers which means that they will give similar simulated deer numbers for the following year. As a result, the simulation set variance will be reduced compared to smaller values of h. The choice of h has other repercussions. If h is zero or close to zero, this means that the simulated posterior parameter values and simulated posterior deer numbers of each simulation set member are treated as if they were independent which amounts to a decoupling of the two.

5.4 Methodological simulation studies

The smoothed bootstrap of simulated posterior model parameters and the linear updating of simulated posterior deer numbers were introduced to make the calculations more efficient and to reduce prediction variances. Some simulation studies were carried out to explore the effects of those measures in simple situations.

5.4.1 Smoothed bootstrap

For i.i.d observations on a parameter of interest sequential estimation will give identical posterior parameter distributions independent of the order observations are used in which is easily verified applying Bayes theorem sequentially. In a simulation study the effects of carrying out a smoothed bootstrap step were explored for this simple case.

Define variable $x \sim N(\mu, 0.005)$ with unknown mean μ which is to be estimated. Two series of observations are given: y ={0.1, 0.3, 0.5} and z={0.5, 0.3, 0.1}. Both data series contain the same values but ordered differently. Sequential estimation by simulation of the unknown mean μ was carried out using data series y and z. Initially, a sample of size 2000 was generated from the prior distribution of μ, which was set to $p(\mu) \sim N(0, 0.025)$. For each sample likelihood weights were calculated and a weighted smoothed bootstrap (h=0.7) was carried out to obtain a sample from the posterior distribution. This led to three sequential samples from the posterior distribution for each data series. The final samples from the posterior distributions should be identical for both data series if the smoothed bootstrap is not biasing results.

Figure 5.2 shows histograms of sequential estimates of the posterior parameter distribution of μ using data series y (top row) and z (bottom row). The final distribution of μ is nearly the same using either data series, which is the average of all data points.

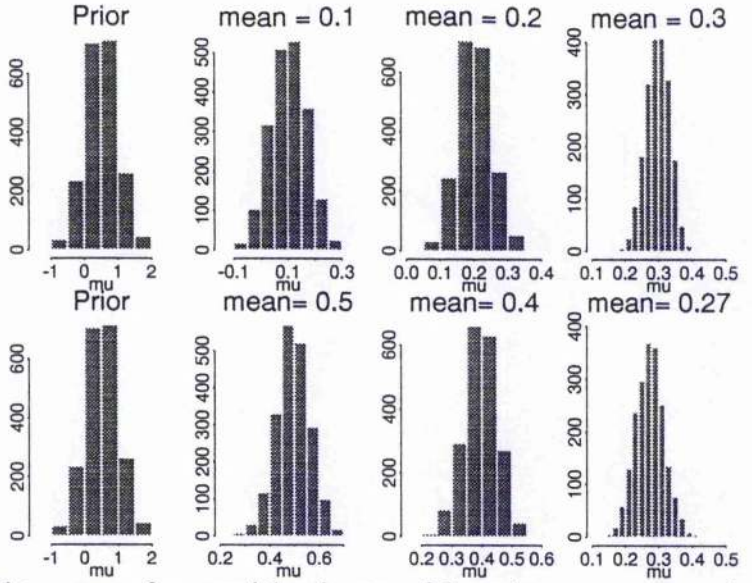


Figure 5.2. Histograms of sequential estimates of the unknown mean μ using data series y (top row) and z (bottom row) and carrying out a smoothed bootstrap after each step.

5.4.2 Updating simulated numbers and smoothing model parameter values

The question of interest is what effect the updating of simulated population numbers and the smoothing of model parameters has on parameter estimation. The example of population counts obtained at different points in time is considered for this. It is assumed that the underlying population growth rate is changing linearly over time. A simple simulation study was carried out to explore the likely consequences.

Define a simple population model $N_{t+1} = N_t \exp(\alpha_t)$, where N_t is the population size at time t and α_t is the growth rate. It is assumed that the population has been counted with error which follows a normal distribution with mean zero and standard deviation 100 and $N_1 = 1000$. The growth rate is assumed to change linearly over time. In population A it is increasing as $\alpha_t = \alpha_{t-1} + 0.01$ with $\alpha_1 = 0.1$ whereas it is decreasing

at the same rate in population B. Twenty years of count data were simulated for both populations and sequential estimation of the growth parameter α_t was carried out smoothing the posterior sample for α_t at each step and either updating simulated values of the population size or not updating them.

Figure 5.3 shows the predicted population size and the sequential estimates of the growth parameter for both populations A and B. Simulated population values were updated for the results presented on the top row of figure 5.3, whereas they were not for the results presented on the bottom row.

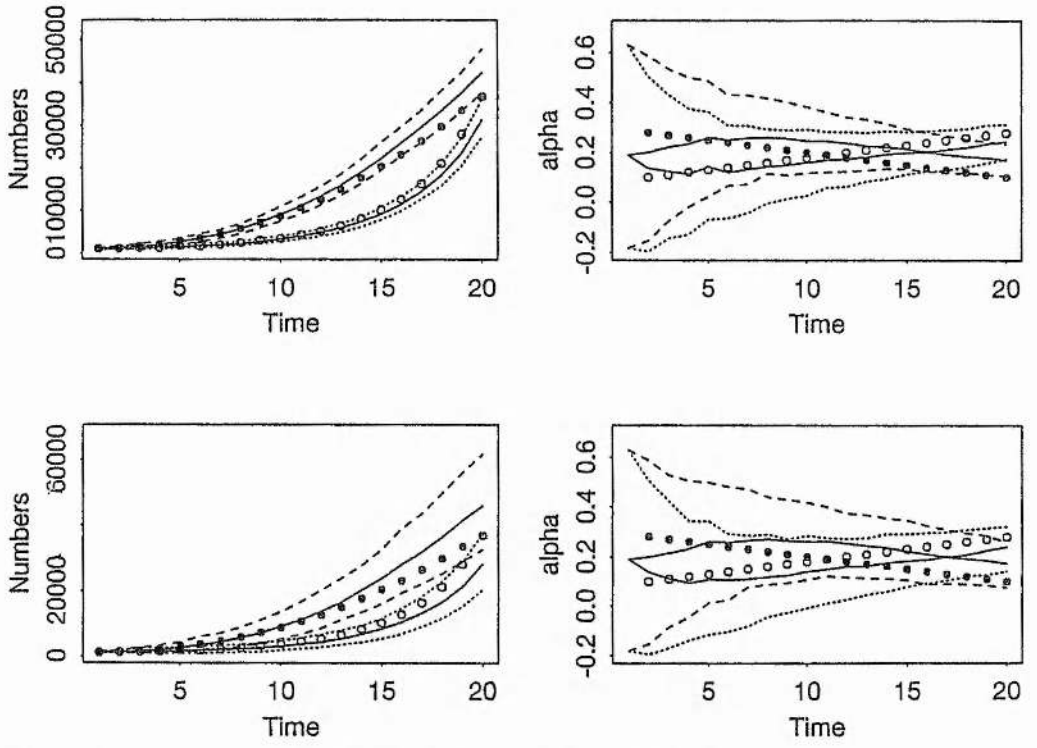


Figure 5.3. Simulation study for estimating population growth parameter α_t. True values are marked by symbols, (○) when α_t was increasing and (●) when decreasing over time. Estimated population numbers and estimates of the population growth rate α_t are presented with 95% confidence intervals (dotted lines for increasing α_t and broken lines for decreasing α_t). Posterior values of α_t were smoothed at each step. Figures on top row show results with updating of simulated population values. Figures on bottom row show results without such updating.

Updating simulated population values led to much tighter confidence intervals for predicted population values and slightly tighter intervals for estimates of the growth rate α_t but no change in its posterior mean. Different posterior distributions were obtained for α_t using population A (increasing true values) and population B (decreasing true values).

5.5 Application to red deer

5.5.1 Population dynamics model for red deer

The life cycle of red deer in Scotland is marked by a number of events. In June, red deer calves are born. During the summer, some of the new born calves die. The stag shooting season takes place during the autumn followed by the hind shooting season in winter. Natural mortality of adults and winter mortality of calves occurs mainly in late winter; the counts are carried out in spring. For the model, the year was defined to start in spring at the time of the counts. The population dynamics model in (5.1) was replaced by

$$\boldsymbol{n}_t = \boldsymbol{S}_t \, (\boldsymbol{R}_t \, \boldsymbol{n}_{t-1} - \boldsymbol{c}_{t-1}) + \boldsymbol{e}_t \qquad (5.7)$$

which incorporates those events, where $\boldsymbol{n}_t$ is the vector of animals in spring of year t and $\boldsymbol{c}_{t-1}$ is the vector of animals shot in the autumn/winter of year t-1 as before. The matrix $\boldsymbol{R}_t$ deals with the ageing of animals, the birth of calves and the survival of their first summer. Natural survival in winter is contained in matrix $\boldsymbol{S}_t$. The subscript t has been dropped in the following description.

$$R = \begin{bmatrix}
0 & \theta_{1,0}(1-\alpha) & \theta_{2,0}(1-\alpha) & \dots & \theta_{11,0}(1-\alpha) & \theta_{12,0}(1-\alpha) & \theta_{13+,0}(1-\alpha) & \theta_{2,1}(1-\alpha) & \dots & \theta_{11,1}(1-\alpha) & \theta_{12,1}(1-\alpha) & \theta_{13+,1}(1-\alpha) & 0 & 0 & \dots & 0 & 0 & 0 \\
1 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\
0 & 1-\theta_{1,0} & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\
 & \vdots & & & & & & \vdots & & & & & & \vdots & & & & \\
0 & 0 & 0 & \dots & 1-\theta_{11,0} & 0 & 0 & 0 & \dots & 1-\theta_{11,1} & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & 1-\theta_{12,0} & 1-\theta_{13+,0} & 0 & \dots & 0 & 1-\theta_{12,1} & 1-\theta_{13+,1} & 0 & 0 & \dots & 0 & 0 & 0 \\
0 & \theta_{1,0} & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\
 & \vdots & & & & & & \vdots & & & & & & \vdots & & & & \\
0 & 0 & 0 & \dots & \theta_{11,0} & 0 & 0 & 0 & \dots & \theta_{11,1} & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & \theta_{12,0} & \theta_{13+,0} & 0 & \dots & 0 & \theta_{12,1} & \theta_{13+,1} & 0 & 0 & \dots & 0 & 0 & 0 \\
0 & \theta_{1,0}\alpha & \theta_{2,0}\alpha & \dots & \theta_{11,0}\alpha & \theta_{12,0}\alpha & \theta_{13+,0}\alpha & \theta_{2,1}\alpha & \dots & \theta_{11,1}\alpha & \theta_{12,1}\alpha & \theta_{13+,1}\alpha & 0 & 0 & \dots & 0 & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 1 & 0 & \dots & 0 & 0 & 0 \\
 & \vdots & & & & & & \vdots & & & & & & \vdots & & & & \\
0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & 0 & \dots & 1 & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 1 & 1
\end{bmatrix}$$

$$S = \begin{bmatrix}
\phi^{*}_{0,0} & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\
0 & \phi_{1,0} & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\
0 & 0 & \phi_{2,0} & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\
 & \vdots & & & & & \vdots & & & & & \vdots & & & \\
0 & 0 & 0 & \dots & \phi_{12,0} & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & \phi_{13+,0} & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & 0 & \phi_{2,0} & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\
 & \vdots & & & & & \vdots & & & & & \vdots & & & \\
0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & \phi_{12,0} & 0 & 0 & 0 & \dots & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & \phi_{13+,0} & 0 & 0 & \dots & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & \phi^{*}_{0,1} & 0 & \dots & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 0 & \phi_{1,1} & \dots & 0 & 0 \\
 & \vdots & & & & & \vdots & & & & & \vdots & & & \\
0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & \phi_{12,1} & 0 \\
0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & \phi_{13+,1}
\end{bmatrix}$$

$$n_1 = \begin{bmatrix}
\text{female calves} \\
\text{yeld hinds 1} \\
\text{yeld hinds 2} \\
\vdots \\
\text{yeld hinds 12} \\
\text{yeld hinds 13+} \\
\text{milk hinds 2} \\
\vdots \\
\text{milk hinds 12} \\
\text{milk hinds 13+} \\
\text{male calves} \\
\text{stags 1} \\
\vdots \\
\text{stags 12} \\
\text{stags 13+}
\end{bmatrix}$$

where $\theta_{a,w}$ is the recruitment rate corresponding to hinds of age a (a = 1,...13+) and status w (w=0 yeld and =1 milk hind), α is the probability of the calf being male. $\phi_{a,x}$ is the annual survival rate of animals of age a (a = 1,...13+) and sex x (x=0 female , x =1 male). $\phi^{*}_{0,x}$ is the calf winter mortality for calves of sex x. Here yeld hinds are hinds aged one year or older that do not have a calf at foot.

The detailed formulation of the population dynamics model was guided by the principle of producing a model fit for its purpose (red deer management) and was not attempting

a perfect description of reality (Starfield, 1997). It is in this spirit that the functions describing survival and recruitment rates have been defined.

Winter calf mortality depends on weather conditions and population density (Clutton-Brock *et al.*, 1987; Guinness *et al.*, 1978). Summer calf mortality is affected by climate (Clutton-Brock and Albon, 1982). However, the aim is to formulate a population dynamics model for exploring the effects of future culling strategies. As the climate in future years is unknown, climatic effects were not considered explicitly but were absorbed into the variance of survival rates. Therefore as an approximation to the observed phenomena the annual natural survival rate of calves is modelled as a function of population density only with no sex difference. Guinness *et al.* (1978) found no overall difference in mortality between male and female calves on Rum. Population density D is standardized to remove correlation between parameters by subtracting the density $\bar{D}_s$, $D^* = D - \bar{D}_s$. $\bar{D}_s$ is the average population density of the data set used for estimating prior parameter values. Calf annual survival rate is

$$\phi_{0,0} = \phi_{0,1} = 1/(1 + \exp(\gamma + \delta D^*)) \qquad (5.8)$$

where γ and δ are the logistic parameters. Female calf winter survival rate is $\phi^*_{0,0} = \sqrt{\phi_{0,0}/k}$ and summer survival rate is $\phi'_{0,0} = \sqrt{\phi_{0,0}\, k}$; k is fixed.

Winter mortality in adult deer is mainly affected by weather (Clutton-Brock and Albon, 1982). However, natural mortality rates also vary with population density (Staines, 1978). As for calves, climatic effects are not considered explicitly and adult annual natural survival rate is modelled as a function of age, sex and population density. Age and density are both standardised by subtracting average values $\bar{a}$ and $\bar{D}_s$ respectively.

$$\phi_{a,x} = \{1 - [\mu_x + (1-\mu_x)/(1+\exp(\eta_x - \lambda_x a^*))]\}\ \{1/(1+\exp(\gamma_x + \delta_x D^*))\} \qquad (5.9)$$

for a=1,...13+, $a^*=a-\bar{a}$, $D^*=D-\bar{D}_s$ and x=0 (female) or 1 (male).

In Scotland, yearling red deer hinds (a=1) only become pregnant at very low population densities. However, in order to model this transition to younger hinds becoming pregnant, a continuous function for the fertility rate involving all age classes, except calves, was chosen. Albon *et al.* (1983) found, that the fertility rate can be described as a logistic function of larder weight. They found different relationships for yeld and milk hinds. Larder weights at the inflexion point of this relationship were different for yeld and milk hinds and were linearly related to population density with different slopes for yeld and milk hinds (Albon *et al.*, 1983). Here it is assumed that this linear relationship between larder weights and population density holds for all fertility rates and not only for the larder weights at median fertility. Furthermore, after investigating the relationships between fertility rates, larder weights and density for both yeld and milk hinds it was decided that assuming identical constant logistic parameter values for yeld and milk hind fertility rates but different relationships with population density provided a satisfying range of plausible curves. Hence the fertility rate functions for yeld and milk hinds have two fixed parameters and two parameters that are to be estimated and describe the relationship with density. Recruitment rate is modelled as fertility rate multiplied by calf summer survival rate as

$$\theta_{a,w} = \phi'_{0,0}\, C/(1+\exp(-B\ \ (W_{a,w} - (A + G_w D^*)))) \qquad (5.10)$$

$W_{a,w}$ is the average larder weight of hinds of age a (a=1,...13+) and status w (w=0 yeld and w=1 milk hind). Population density D is standardised as $D^*=D-\bar{D}_f$ where $\bar{D}_f$ corresponds to the density at which the parameters for (5.10) were estimated.

A summary of all demographic parameters and the functions used to model them is

given in table 5.1. The function type gives the function with respect to the function arguments. For example, function f_2(age-$\bar{a}$, population density-$\bar{D}_s$) consists of a logistic function of standardised age and a logistic function of standardised population density.

The detailed population dynamics model for red deer (5.7) contains complex functions for survival and recruitment rates with a great number of parameters. Given the count observations which do not distinguish between age classes nor yeld and milk hinds, the updating algorithm will provide samples from the joint posterior distribution but many individual parameters will not be estimable as parameters will be confounded. As a consequence, marginal posterior parameter estimates for individual parameters will not be meaningful. However, the set of combinations of parameter values that give good predictions is still valid. It is this set of parameter values that will constitute the calibrated population dynamics model and will be used for exploring management options in chapter 6.

For real cull data, animals are sometimes aged reasonably accurately, but are often merely tallied by the three categories used for counting: stags, hinds and calves (Trenkel *et al.*, in press). When real data were used, culled animals were assigned to age categories by assuming that no age-selective culling took place for stags and hinds.

Table 5.1. Summary of functions and their parameters used in the red deer population dynamics model. Numbers refer to equations in text.
* See text

Demographic parameter	Function	Function type*	Fixed parameters (assumed known)	Parameters to be estimated
probability calf is male				α
calf annual survival	f_1(population density-$\bar{D}_s$) (5.8)	logistic	$\bar{D}_s$	γ, δ
calf summer survival	$\sqrt{f_1(.)\ k}$		k	
calf winter survival	$\sqrt{f_1(.)/k}$		k	
hind winter survival	f_2(age-$\bar{a}$, population density-$\bar{D}_s$) (5.9)	logistic, logistic	$\bar{a}$, $\bar{D}_s$	μ_0, η_0, λ_0, γ_0, δ_0
stag winter survival	f_3(age-$\bar{a}$, population density-$\bar{D}_s$) (5.9)	logistic, logistic	$\bar{a}$, $\bar{D}_s$	μ_1, η_1, λ_1, γ_1, δ_1
yeld hind fertility	f_4(larder weight, population density-$\bar{D}_f$) (5.10)	logistic, linear	C, B, $\bar{D}_f$	A, G_0
milk hind fertility	f_5(larder weight, population density-$\bar{D}$) (5.10)	logistic, linear	C, B, $\bar{D}$	A, G_1

5.5.2 Prior parameter distributions and parameter values

Independent normal prior distributions were defined for most model parameters with the exception of C, B and k which were assumed to be constant. In general, mean values of prior distributions were estimated from data or taken from the literature and variance estimates were chosen to give reasonably wide prior distributions.

Survival rates for adult red deer in Scotland can be estimated by combining three sources of data. The first data set was collected by the Deer Commission for Scotland (DCS) on the island of Rum between 1986 and 1994. Once every spring the whole island was searched for dead animals and the age and sex of any animal they found was recorded. Dead calves were not sexed. Secondly the DCS counted the number of stags, hinds and calves in spring on Rum over the same time period. The third data set was the reconstructed red deer population on Rum for the years 1957-61 (Lowe, 1969). Lacking any information about the actual age structure of the population at the time of the mortality data set, that is from 1986 to 94, it was assumed that the average age structure during the years 1957 to 61 was the best available estimate. The total number of hinds and stags counted between 1986 and 94 were split into age classes based on the average age structure of the reconstructed population. Annual mortality rates by age class were calculated dividing the number of animals found dead in an age class in year t by the sum of estimated number of animals in this age class present in the same year's count (year t) and the number of animals found dead. This approach assumes that natural mortality will occur after culling mortality. No adjustment was made to correct for the fact that some animals died but were not found. Thus, the natural mortality rates calculated this way underestimate the true rates. The sex ratio of male to female calves

at birth was found to be around 0.5 at Glenfeshie (Mitchell *et al.*, 1986) and around 0.52 for calves born to hinds on Rum aged five years and older (Clutton-Brock *et al.*, 1997). Here the value of 0.52 was chosen as the mean for the prior distribution.

Albon *et al.* (1983) fitted logistic functions to fertility rates and larder weights from several areas in Scotland: Glen Dye, Invermark, Glenfeshie, Rum and Scarba. The values chosen for the logistic parameters C and B are based on average values for yeld and milk hinds and all areas. From the plot of larder weight at median fertility vs. total deer density the means for density relationships of the fertility rates were read off (Albon *et al.*, 1983, Fig. 5). Average larder weights at age for yeld and milk hinds shot at Glenfeshie (Mitchell *et al.*, 1986) were used even for the case studies as no local information was available. Table 5.2 summarises the values used for constant parameters and table 5.3 the prior distributions defined for unknown parameters.

Table 5.2. Values used for constant parameters in red deer population dynamics model.

Parameter	Value	Source/Data set
$\bar{D}_s$	18.3	DCS Rum data
$\bar{a}$	8.0	DCS Rum data
k	0.94	after Clutton-Brock *et al.* 1985
$\bar{D}_f$	15.2	Glenfeshie, Albon *et al.* 1983, fig.5
C	0.88	after Albon *et al.* 1983
B	0.25	after Albon *et al.* 1983
W_a a=1,..,13+		hinds shot at Glenfeshie 1966-75, Mitchell *et al.* 1986

Table 5.3. Prior parameter distributions and data sources used to define means and variances. $\mu'_x = \log(\mu_x/(1-\mu_x))$

Parameter	Distribution	Mean	Variance	Source/Data set
γ	normal	-0.68	0.08	DCS Rum data, Lowe 1969
δ	normal	0.05	2.0×10^{-6}	DCS Rum data, Lowe 1969
γ_0	normal	-5.47	2.1	DCS Rum data, Lowe 1969
δ_0	normal	0.63	0.35	DCS Rum data, Lowe 1969
μ'_0	normal	-3.89	0.3	estimate
η_0	normal	5.08	1.41	DCS Rum data, Lowe 1969
λ_0	normal	0.99	0.08	DCS Rum data, Lowe 1969
γ_1	normal	-6.35	2.2	DCS Rum data, Lowe 1969
δ_1	normal	0.8	0.31	DCS Rum data, Lowe 1969
μ'_1	normal	-3.89	0.4	estimate
η_1	normal	5.52	1.4	DCS Rum data, Lowe 1969
λ_1	normal	0.81	0.058	DCS Rum data, Lowe 1969
A	normal	41	2	after Albon *et al.* 1983, fig.5
G_0	normal	0.56	0.05	after Albon *et al.* 1983, fig.5
G_1	normal	0.31	0.03	after Albon *et al.* 1983, fig.5
α	normal	0.52	4×10^{-5}* 1×10^{-3}#	mean after Clutton-Brock *et al.* 1997, hinds aged 5+ in table A1

* used for case studies 1 & 2
\# used for simulation studies

Initial simulated deer numbers, $v_{j,1}$, were obtained in several steps. Firstly, for stags, hinds and calves random samples were drawn from normal distributions centred on the counts at time t=1 with coefficients of variation V equal to ten percent for adults (see chapter 3) and 15% for calves, $\gamma_1 \sim N(x_1, (Vx_1)^2)$. Secondly, for both stags and hinds, the probability for the number of animals in age class b was obtained by random selection of one of three possible age distribution curves (Figure 5.4).

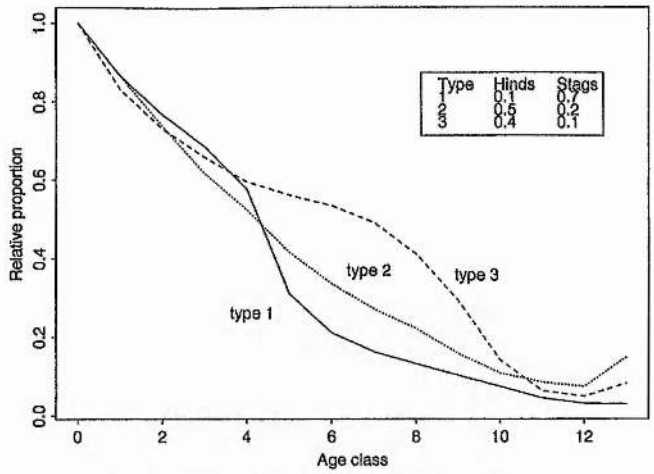


Figure 5.4. Three hypothetical age distribution curves for red deer populations. Type 2 is similar to the distribution reconstructed on Rum (Lowe, 1969). Type 1 was created to reflect a population that has been culled heavily from age 4 onwards. Type 3 was assumed to reflect a population where mainly older animals have been culled (age eight onwards). Numbers indicated the probabilities assigned to each of the curves for stags and hinds. The age group 13 contains all animals 13 years and older.

The numbers given in figure 5.4 were rescaled in proportion to the number of calves and adults selected previously to obtain probabilities b_a for each age class a. This ensures a smooth transition between the created number of calves and older age classes. The simulated deer numbers in each age class were obtained by performing independent Bernoulli trials using the selected age probabilities, $\nu_{b,1} \sim Bin(\gamma_{j,1}, b_a)$. The use of independent Bernoulli trials instead of drawing from a multinomial distribution increased the variance of initial population numbers slightly. Hind numbers in each age group were further divided into hinds with calf and those without assuming the proportion of milk hinds to be zero for age b=1 & 2, 0.3 for b=3, 0.6 for b=4 and 0.9 for older hinds unless this meant that the number of all milk hinds was larger than the number of calves in which case the oldest hinds were assumed to be yeld. For calves, a Bernoulli draw with p=0.5 was used to determine the sex.

An estimate of the variance-covariance matrix of the counting error is needed for the likelihood function (5.4). In the study of repeat census counts on Rum (chapter 3), the variance of the counting error was estimated to be about 10% for stags and hinds and larger for calves (see chapter 3). This size of counting error was assumed for adult animals whilst it was set to 15% for calves. The covariances of the counting error and of predicted numbers were set to zero.

There are a number of issues that are important for the success of the updating algorithm. The consistency and precision of predictions and marginal (posterior) parameter estimates are affected by them. They are the smoothing factor, the linear updating of posterior deer numbers, the size of the simulation set, especially at the initialisation step, the distance between the prior and the joint posterior parameter distribution and the dimension of the parameter space. A high dimensional parameter space requires a large simulation set in order to cover it. The deer model has 16 parameters that are estimated, which is a large parameter space. An additional complication in the case of the red deer model is that some parameters are confounded which makes those parameters not estimable. These issues will be considered in the following simulation and case studies.

5.5.3 Simulation studies

The choice of the smoothing factor h in the smoothed bootstrap of model parameters was investigated empirically and the benefits of updating simulated deer numbers were looked at. The parameter values used for simulating populations are given in Table 5.4.

Table 5.4. Parameter values (5.8 & 5.9) used for simulated populations.
Area =150 km^2; $\mu'_x = \log(\mu_x/(1-\mu_x))$ for x=0 (female adults) and x=1 (male adults).

Calf survival rate			Hind survival rate			
γ	δ	λ_0	η_0	γ_0	δ_0	μ'_x
-0.62	0.07	0.8	4.6	-1.28	0.75	-3.89

Stag survival rate				Fertility rate			Sex
λ_1	η_1	γ_1	δ_1	A	G_0	G_1	p(male)
1	6	-0.53	0.9	45	0.66	0.4	0.5

Size of simulation set

Some simulations were carried out to investigate the relationship between the likelihood weights (5.4) in the updating algorithm and the size k of the simulation set at time t=1. A small data set with two counts and one cull (first two years for Islay data, see section 5.5.5) was used for these investigations and eleven levels for k : 500, 1000, 2000, ..., 10,000 with ten repeats for each level. For all levels of k, the average percentage of simulation set members selected at least once by the weighted bootstrap was about 36% and 12.6% of set members carried 60% of the weights on average (Figure 5.5).

a) b)

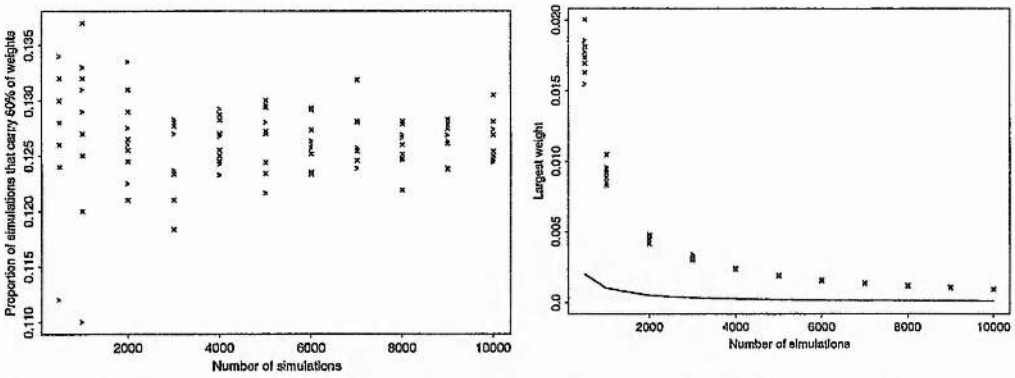


Figure 5.5. a) Proportion of simulation set members carrying 60% of likelihood weights at time t=2 in simulation study plotted over size of simulation set used. b) Size of largest likelihood weight for same simulations. The line gives the average weight.

These results apply to the particular data set only as the necessary simulation set size depends on the distribution of the likelihood weights which in turn will be different for different count data sets. Hence, general conclusions cannot be drawn but the results give an indication for the kind of results to be expected for other red deer populations. Based on these simulations, for k=2000, which ensures a reasonable speed for the updating algorithm, one would expect 252 simulation members to carry 60% of the weights and 720 sets to be represented in the posterior simulation set Ψ_2^{**} which is a sample from the joint posterior distribution at time t=2. The size of all simulations sets was set to 2000 for all subsequent investigations.

Smoothing factor

The value of the smoothing factor h affects the estimate of the variance of predicted deer numbers. For small simulation sets, repeated runs of the updating algorithm will produce different one year ahead predictions. Ideally, the component of the prediction

variance due to repeated runs of the updating algorithm should be negligible so that the variance of the simulation set can be used to estimate the prediction variance. Therefore, as a selection criterion for the value of the smoothing factor h it is suggested to look at the variance components of simulated deer numbers at time t.

Three levels of smoothing factors were used in the simulations: h=0, 0.7 and 0.9. Fifteen years of population data were simulated and each year of each population was sampled with a coefficient of variation of 10% to obtain time series of "counts" for stags and hinds and 15% for calves. It was assumed that no animals would be shot. The updating algorithm was then applied to each time series of "counts" and simulated one year ahead deer numbers were obtained. By repeatedly running the updating algorithm for different random seed values, estimates for the between run prediction variance were obtained. Repeating the simulation process for a number of different count series from different stochastic realizations of simulated populations gave estimates for the parts of the prediction variance due to counting variability and population stochasticity. The overall structure of the simulation design was nested with five population realizations simulated from the same set of parameter values, two sets of counts within each population realization, two runs of the updating algorithm for each set of "counts" with simulation sets of size 2000.

The variance components due to different sources were estimated by performing an analysis of variance (Scheffé, 1959) on the simulated deer numbers. Consider the following random effects model for simulated deer numbers v at time t

$$v_{pcbw}(t) = \mu(t) + p_p(t) + c_{pc}(t) + r_{pcb}(t) + s_{pcbw}(t) \qquad (5.10)$$

for p=1,...,5; c=1,2; b=1,2; w=1,...,2000.

μ is the overall mean, p_p is the population effect representing stochastic birth and death processes, $c_{p,c}$ is the counting effect, $r_{p,c,b}$ the between runs effect and $s_{p,c,b,w}$ the within run effect. Hence, based on this model the variance of simulated numbers can be split into four components: population variance σ_P^2, counting variance σ_C^2, between run variance σ_B^2 and within run (=simulation set) variance σ_W^2. Table 5.5 gives the sums of squares and expected mean squares for the random effects model for simulated deer numbers at time t.

Table 5.5. Sums of squares and expected mean squares for random effects model (nested design) for simulated deer numbers at time t. d.f. = degrees of freedom. Variance source: P= population, C=counts B= runs and W=simulation sets.

Sums of squares	d.f.	Expected mean squares
$SS_P = 2 \cdot 2 \cdot 2000 \sum_p (v_{p...} - \bar{v}_{....})^2$	5-1	$2 \cdot 2 \cdot 2000 \cdot \sigma_P^2 + 2 \cdot 2000 \cdot \sigma_C^2 + 2000 \cdot \sigma_B^2 + \sigma_W^2$
$SS_C = 2 \cdot 2000 \sum_p \sum_c (v_{pc..} - \bar{v}_{p...})^2$	$(2-1) \cdot 5$	$\sigma_W^2 + 2000 \cdot \sigma_B^2 + 2 \cdot 2000 \cdot \sigma_C^2$
$SS_B = 2000 \sum_p \sum_c \sum_b (v_{pcb.} - \bar{v}_{pc..})^2$	$(2-1) \cdot 2 \cdot 5$	$\sigma_W^2 + 2000 \cdot \sigma_B^2$
$SS_W = \sum_p \sum_c \sum_b \sum_w (v_{pcbw} - \bar{v}_{pcb.})^2$	$(2000-1) \cdot 2 \cdot 2 \cdot 5$	σ_W^2

To test for a significant run effect at time t, the ratio of the mean squares for between run variation to within run variation, $\frac{SS_B/10}{SS_W/39980}$, was calculated for different smoothing factors. This ratio corresponds to an F-test on 10 and 39980 degrees of freedom. For all values of h and t=1,...15, this test was highly significant. The F-test for a counting effect at time t on 5 and 10 degrees of freedom, $\frac{SS_C/5}{SS_B/10}$, was not significant for all values of h and number of years of counts, t=1,...15.

In this simulation study, the variance of simulated deer numbers at time t is the sum of the four variance components

$$\sigma_v^2(t) = \sigma_P^2(t) + \sigma_C^2(t) + \sigma_B^2(t) + \sigma_W^2(t) \qquad (5.11)$$

However, as the test for a counting effect was not significant (null hypothesis $\sigma_C^2(t)=0$), the counting variance component can be ignored. If the variance for a given population realisation is considered, which would be the case for a real red deer population, the first component in (5.11) disappears as well and $\sigma_v^2(t)$ becomes the sum of the between runs and simulation set variance components. This means that for any value of h, if the variance of simulated deer numbers is estimated by the simulation set variance only, the result will be negatively biased.

The bias in the variance of simulated deer numbers when estimated by the simulation set variance was defined as $\frac{\sigma_W^2}{\sigma_B^2+\sigma_W^2} - 1$. The size of the bias is plotted in figure 5.6 for all time steps and values of the smoothing factor. It depended on the smoothing factor h and was of the order of 5% (8% for calves) for $h = 0$ or 0.7 for the majority of time steps. In these simulations, four to five years of counts used in the updating algorithm led to the largest bias which corresponds to a large between run variation. Using more counts reduced the between run variance component for all categories apart from calves.

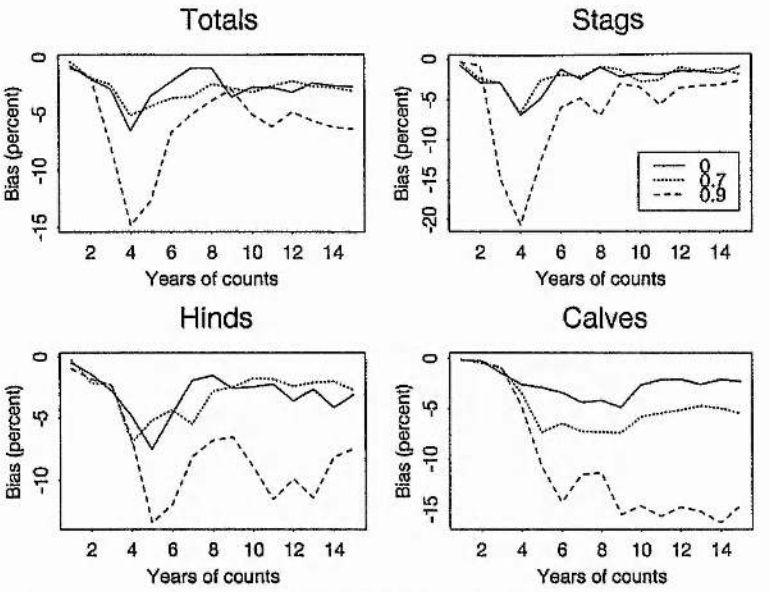


Figure 5.6. Percentage bias in the prediction variance when the variance of the simulation set is used as an estimator plotted against numbers of counts used in the updating algorithm for each of four groupings of animals. Figures show ratios for three values of the smoothing factor.

Based on this simulation study, a value of 0.7 for h seems to be suitable as it allows estimation of the prediction variance by the simulation set variance with only small negative bias. The analysis of variance table with h=0.7 for the simulated deer numbers in the 8th year after having used seven years of counts is given in Table 5.6. In the analysis of variance table, the prediction variance for the total number of deer based on the simulation set variance was 4.1×10^4 whereas it would be 4.3×10^4 ($=4.1\times10^4 + (384\times10^4-4.1\times10^4)/2000$ taking the between run variance into account.

Table 5.6. Analysis of variance table for simulation study with smoothing factor h=0.7 for the smoothed bootstrap of posterior model parameter values. The mean squares are for the simulated deer numbers at t=8 after having used seven years of counts in the updating algorithm.

Source	Degrees of Freedom	Mean squares of simulated deer numbers ($x10^4$)			
		Total	Stags	Hinds	Calves
Population	4	2031	266	2127	126
Counts	5	186	42	103	9
Runs	10	384	26	138	30
Simulation set	39980	4.1	1.6	1.7	0.1

Linear updating of posterior simulated deer numbers

The linear updating of posterior simulated deer numbers is intended to reduce one year ahead prediction errors. As the weighted bootstrap provides samples from the posterior distribution of deer numbers it was of interest to find out what gain if any might be achieved by the additional linear updating. A simulation study was carried out to compare mean square prediction errors for three linear updating methods. Firstly, posterior simulated deer numbers were updated using variance ratios as described. Secondly, posterior simulated deer numbers were not updated; and thirdly, all simulation set members were set to the observed counts.

Stochastic populations were simulated for 10 years and predicted deterministically for the 11th year. Each of the ten years was sampled with a coefficient of variation of 10% to obtain time series of annual simulated counts. These were then used in the updating algorithm with smoothing factor h=0.7. One year ahead predictions (11th year) were

obtained for each simulated count series. Predicted numbers were compared to true (deterministic) population values giving mean square prediction errors. Results are averages of 30 runs (Table 5.7).

Table 5.7. Mean square error of one year ahead predictions in different categories when posterior simulated deer numbers were either updated (variance ratios), not updated or set to the observed counts. Results are expressed in proportion to the mean square error of the results with linear updating proportional to the variance ratio. The results were obtained by running the updating algorithm on ten years of simulated counts and comparing the predictions for the 11th year with the true population value.

Updating type	Prediction category			
	Total	Stags	Hinds	Calves
Variance ratios	1	1	1	1
No updating	1.66	1.30	1.83	1.01
Counts	2.26	2.13	1.75	1.17

For all animal categories, the mean square error was smallest when posterior simulated deer numbers were updated using variance ratios. For the other two updating types, no updating at all was generally better than setting the simulated counts to the observed counts.

Performance of updating algorithm for simulated data

The performance of the updating algorithm was evaluated on a simulated population which was generated stochastically with parameters values as in table 5.4. Fifty years of population data were simulated and counts generated by sampling randomly from the population (normal distributions with 10% coefficients of variation for adults and

15% for calves). The updating algorithm was run with prior distributions as in tables 5.2 and 5.3 and with h=0.7 and k=2000.

Predicted population numbers and simulated counts disagreed substantially for the first four to five years (Figure 5.7) but after this, average predicted deer numbers got closer to the simulated counts. All counts lay between the 2.5 and 97.5 percentile points of predicted deer numbers in later years which seems unexpected as one would expect on average 5%, that is 2 counts for a 40 year period, to lie outside. This also occurred in repeated runs which seems to indicate that the confidence intervals obtained as percentile points by the updating algorithm are slightly too large. It was noted before (section Smoothing factor) that the choice of the smoothing factor h in the smoothed bootstrap of model parameters has an impact on the prediction variance. The value of the smoothing factor was chosen in an *ad hoc* manner in order to give consistent results across repeated runs but it also affects prediction confidence intervals in a somewhat uncontrolled way. This interaction between the value of the smoothing factor and the prediction variance will be explored further in a simulation study.

As some of the parameter values used for the simulated population were not in the centre of the prior distributions (two parameter values were far out in the tails of the prior distributions) it took a number of years before predictions improved. Despite this difference between the mean of prior distributions and the true parameters, the updating algorithm led to a set of parameter values that were able to give good predictions on average.

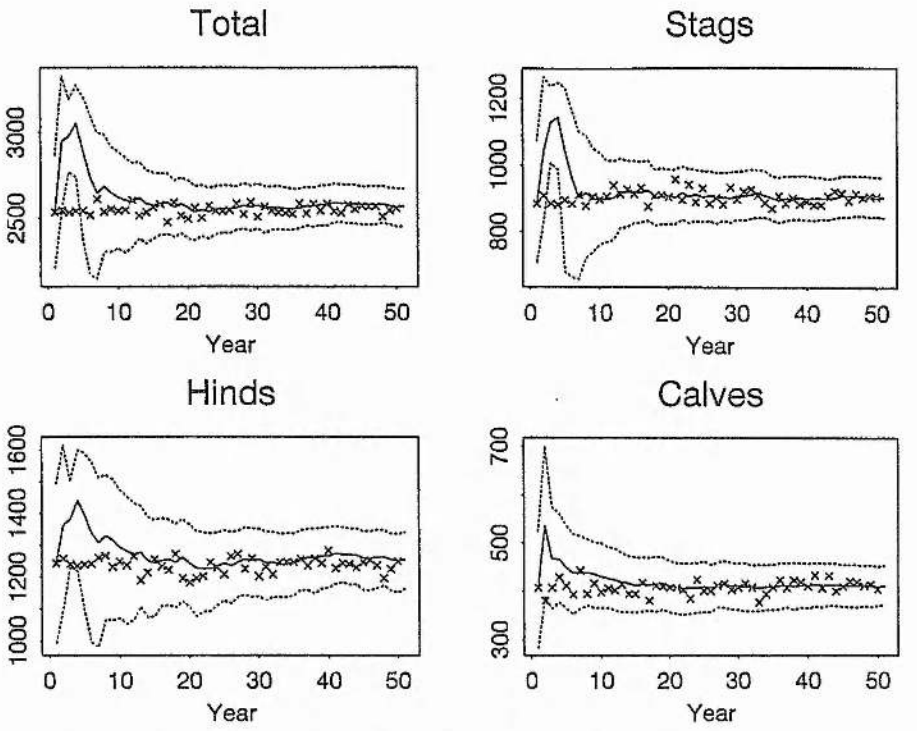


Figure 5.7. Calibrating the population dynamics model using simulated data. Plots show one year ahead predictions of population numbers with 95% confidence intervals for population numbers (dotted lines). Simulated counts x.

As pointed out before, many parameters are confounded which means one expects differences between marginal posterior parameter estimates and the true values. True parameter values are not known for real population and these discrepancies would not be obvious. This simulation study gives the opportunity to compare true values with posterior parameter values to see which parameters are more estimable than others given the true values and the prior distributions.

Density estimates of prior and marginal posterior parameter values obtained after using 50 years of simulated count data are given in figure 5.8. The mode of the posterior values for the intercept of the calf survival rate function (eq. 5.8), gamma(calves), was

close to the real value of minus 0.6. In contrast, the posterior values for the slope of the same function, delta(calves), were smaller than prior values and thus even further from the true value of 0.07. This was the one of the parameters where the true value was situated far out in the tail of the prior distribution. As the population density of the simulated counts was about constant, no information was supplied about the parameter delta(calves) which describes the relationship with density though the precision of its posterior estimates appear to be increased compared to the prior. This example shows that the width of the posterior distribution does not allow any conclusions about the accuracy of the point estimate. The mode of posterior values for the maximum hind survival in (eq. 5.9), mu'(hinds), was smaller than the true value (-3.89), which was identical to the mode of the prior. The posterior values for the slope of the hind survival rate relationship with age were very similar to prior values. The mode of the posterior values for the intercept, eta(hind) was close to zero, which is far from the true value of 4.6. The posterior values of the two parameters relating hind survival to population density, gamma(hinds) and delta(hinds), have been moved towards the true values, but a mode of -4.5 for gamma(hinds) is still far from the true value of -1.3. Posterior variances were slightly reduced for both parameters. The posterior parameter values for the maximum stag survival rate (eq. 5.9), mu'(stags), were centred at minus 1.5 which is far from the true value (-3.89). The mode of posterior values for the parameters of the logistic relationship of stag survival with age, lambda(stags) and eta(stags), were nearly unchanged from the prior values in the first case (true value 1.0) and shifted towards the true value 6.0 in the second case. As for hinds, the posterior values of the stag survival rate parameters for the relationship with population density, gamma(stags) and delta(stags), were wrong. The modes of posterior values were further from the true values than the priors. The parameters of the fertility rate (eq.

5.10) for yeld hinds were well estimated. The posterior values for A and G(yeld hinds) were centred on or close to the true values. The posterior values of the parameter in the relationship of fertility with population density for milk hinds, G(milk hinds), were nearly identical to the values for yeld hinds and thus too large (true value 0.4). The data did not contain separate information for yeld and milk hinds, which might help to explain this observation. Finally, the posterior values for the probability that a calf is male were centred on the true value (0.5).

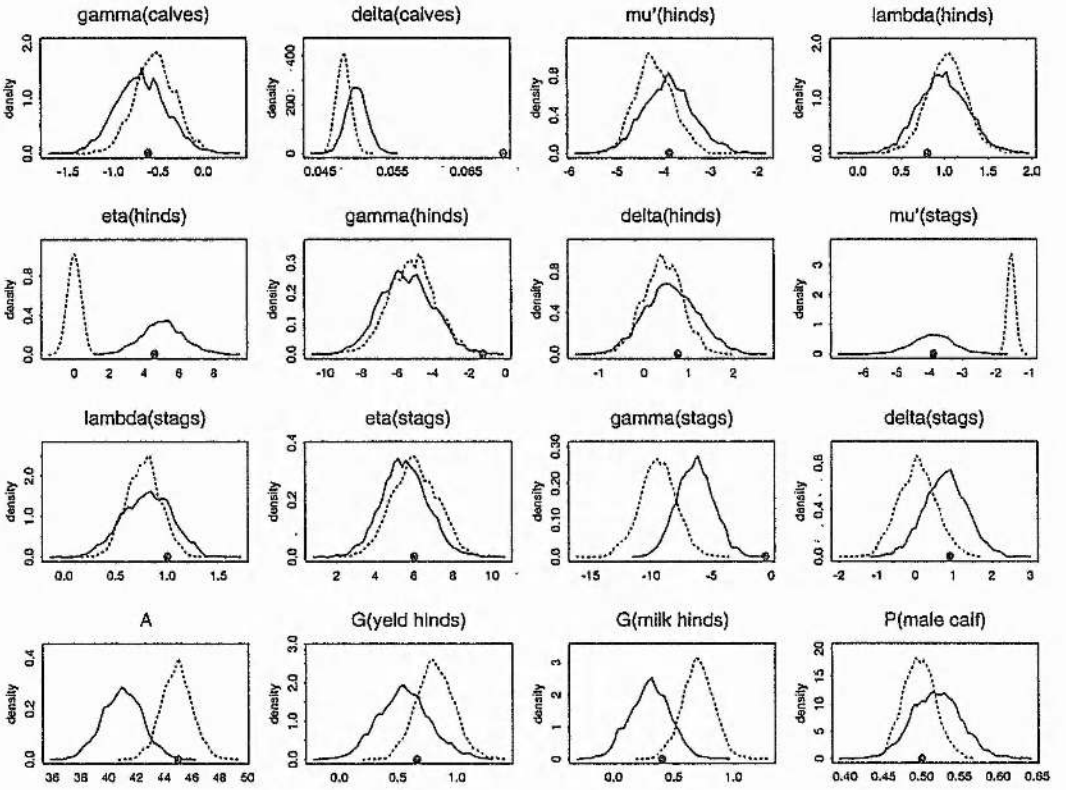


Figure 5.8. Density estimates for prior parameter values (solid line) and posterior parameter values (broken lines) obtained after using 49 years of simulated data. True values are indicated as ●.

Compared to the parameter values used for simulating the population, some of the individual marginal parameter values were not centred on the true values. This is the result of confounded parameters which is illustrated by survival and fertility rates

resulting from the prior and posterior parameter values (Figure 5.9). Posterior hind survival rates were lower for older hinds compared to the survival rates obtained from prior parameter values. This resulted in fewer hinds surviving. For stags, the maximum posterior survival rate was about 0.8 with about the same value for all age classes. The overall effect was that fewer stags survived. Hence, posterior parameter estimates for both hind and stag survival rates resulted in reduced survival rates compared to the priors, but this was achieved by changing different aspects of the survival rate function. This illustrates that parameters in the survival rate functions are confounded.

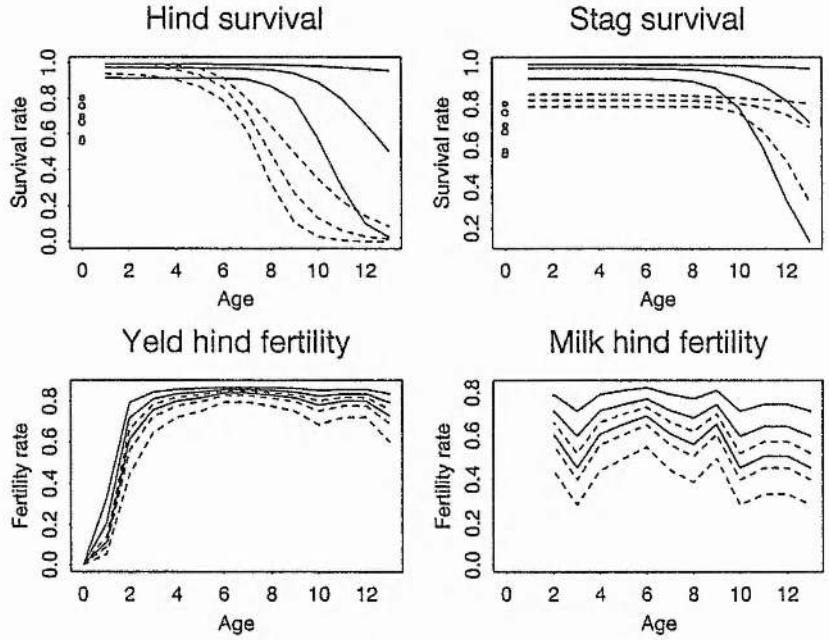


Figure 5.9. Prior (solid lines for adults & closed symbols for calves) and posterior (broken lines for adults & open symbols for calves) survival and fertility rates at a population density of 15 deer per km^2 obtained after using 49 years of simulated data. Figures show 95% confidence intervals.

Some of the true parameter values fell in the tails of the prior parameter distributions in this simulation study and the posterior parameter values were not centred on the true

values in general. The effect of confounded parameters on parameter estimation was highlighted for the parameters in the stag and hind survival rate functions. However, this example showed that even under those circumstances the updating algorithm can identify a set of parameter values which lead to good predictions of red deer numbers after a small number of years as shown in figure 5.7.

For comparison with the above simulation study, the updating algorithm was run for an example of simulated population counts from a population whose demographic parameter values corresponded to the mean values of all prior parameter distributions. Fifty years of population data were simulated stochastically and sampled to obtain a time series of counts as described for the previous simulation study.

Density estimates of prior and marginal posterior parameter values obtained after using 50 years of those simulated counts are given in figure 5.10. The mean of most but not all marginal parameter distributions stayed unchanged compared to the prior values and a reduction in variance occured in some cases. The observed shift in the mean of some of the parameter distributions might be due to the relatively small simulation set size which was used and might become less pronounced or disappear if larger simulation sets could be used which was not the case here.

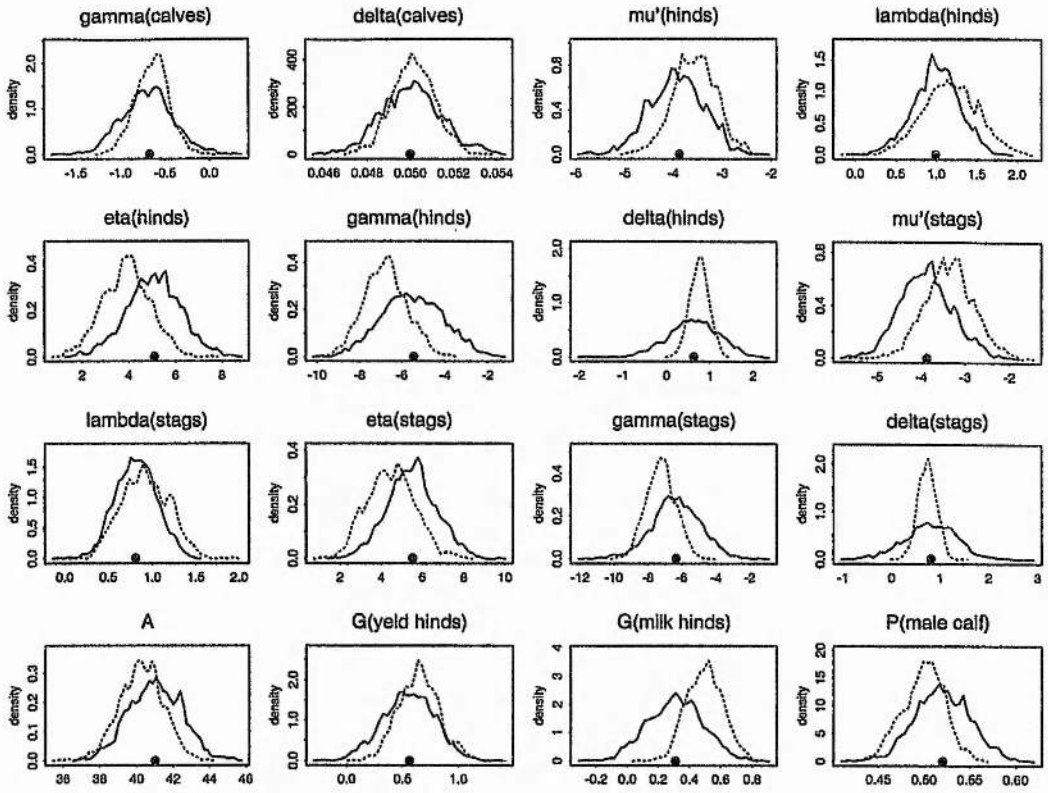


Figure 5.10. Density estimates for prior parameter values (solid line) and posterior parameter values (broken lines) obtained after using 49 years of simulated data. True values are indicated as ●.

Impact of smoothing factor on prediction confidence intervals

In the simulation study of the previous section it was noted that the prediction confidence intervals seemed to be too large. One possible explanation was that the width of the prediction confidence interval was affected by the value of the smoothing factor in the smoothed bootstrap of model parameters. A simulation study was carried out to look at this relationship more closely and gain an understanding of the possible difference in prediction confidence intervals due to different values of the smoothing factor.

As in previous studies, population data were simulated stochastically by carrying out random draws in order to determine the actual number of animals surviving and being born every year. By setting demographic parameters equal to the mean prior parameter values it was hoped to avoid any effects due to parameters being in the tails of the prior distributions. Count data were obtained in the usual fashion. The updating algorithm was run with three different smoothing factors. The smoothing factor was set to zero (maximal smoothing), 0.7 (usual value) and 1 (no smoothing).

If no smoothing of model parameter values is carried out, the parameter values of all simulation sets become equal after a number of years, the variances of posterior parameter values become zero and the updating algorithm fails at that point. In the simulation study this happened after 18 years of count data had been used. Hence, predicted deer numbers with 95% confidence intervals obtained for the three different smoothing factors are only given for 18 years (Figure 5.11). Prediction confidence intervals became noticeably smaller as less smoothing was carried out (top to bottom in figure 5.11). This seems to support the explanation put forward regarding the width of the prediction confidence intervals. However, none of the counts lay outside the 95% confidence intervals which would actually not be expected given the length of the data series and discounting the first couple of years as adaptation phase. There are several possible causes for this adaptation phase. Although the simulated population had parameter values identical to the mean prior parameter values, the initial age structures differed and there was also the assumed counting error. Future work should consider in more detail the choice of the smoothing factor and the appropriateness of the prediction confidence intervals provided by the updating algorithm.

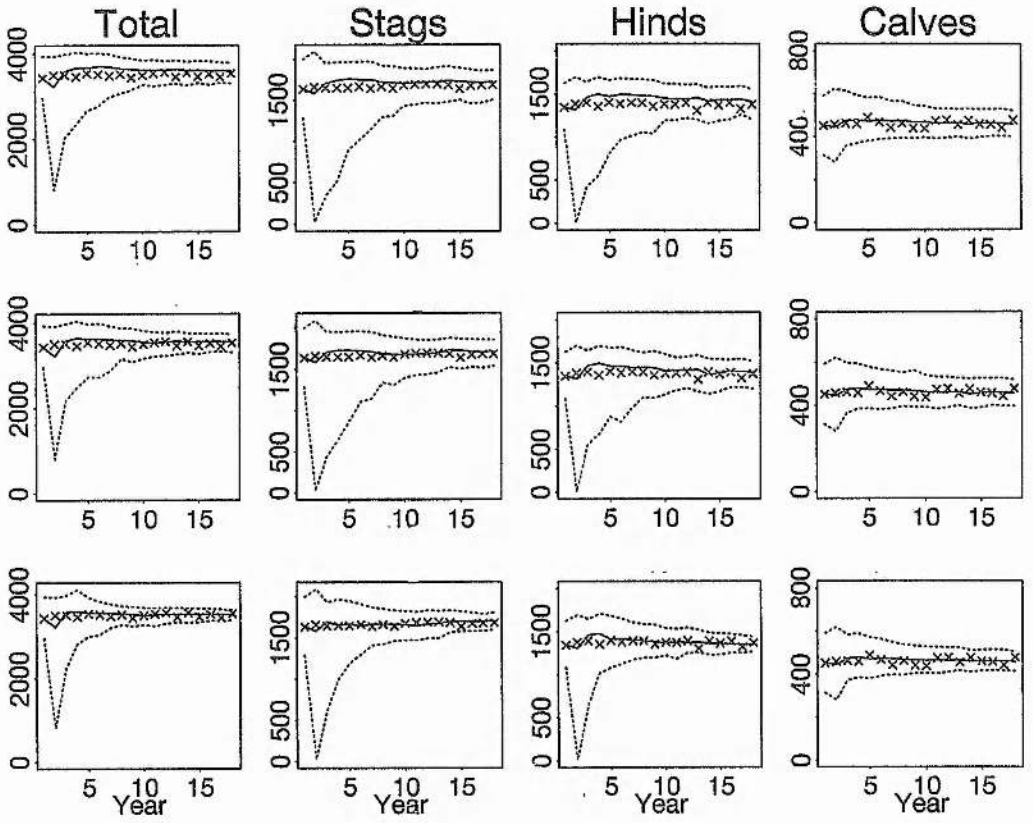


Figure 5.11. Calibrating the population dynamics model using simulated data (population parameter values equal to mean of priors). Plots show one year ahead predictions of population numbers with 95% confidence intervals for population numbers (dotted lines). Simulated counts x. Results are for calibration with smoothing factor h=0 (top row), h=0.7 (middle row) and h=1 (bottom row).

5.5.4 Case study 1

Background

The performance of the proposed updating algorithm was evaluated for a red deer population in Caithness and Sutherland. The population was counted in 1987 by the Deer Management Group of that area and then annually from 1992 to 1995 (Table 5.8). The numbers of stags, hinds and calves culled during these years was recorded. As no age specific culling rates were available it was assumed that different age classes were

shot unselectively. The count in 1987 was used to create starting populations. A smoothing factor h=0.7 and a simulation set of size 2000 were used.

Table 5.8. Historical data for red deer population in Caithness and Sutherland (source R. McNicol).

	COUNT			CULL		
Year	Stags	Hinds	Calves	Stags	Hinds	Calves
1987	2729	5489	2105	394	644	152
1988	-	-	-	439	815	159
1989	-	-	-	461	1165	266
1990	-	-	-	462	1141	286
1991	-	-	-	501	1075	334
1992	4768	5363	2273	596	1644	551
1993	4780	5299	2169	588	1597	446
1994	5196	4719	1299	640	917	243
1995	4077	4029	1683	-	-	-

Calibration results

The population dynamics model was calibrated for this population. To assess whether there was any between run variation in the one year ahead predictions which would indicate that the size of the sample set might not have been large enough, the updating algorithm was run for three different seed values. Counts and the annual one year ahead predictions of population numbers are given in Figure 5.12. The estimated deer numbers and confidence intervals were nearly identical for the three repeat runs.

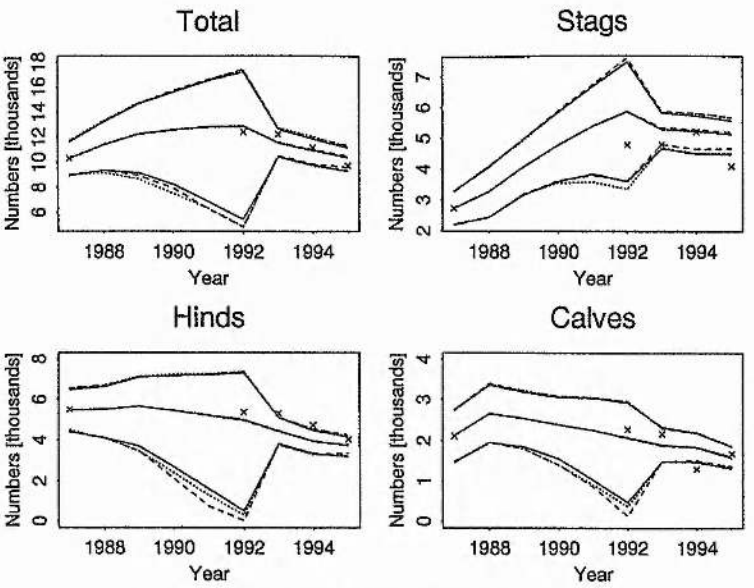


Figure 5.12. Calibrating the population dynamics model using data from red deer population in the far North-East of Scotland. One year ahead predictions of population numbers with 95% confidence intervals for three repeat runs of the updating algorithm. Observed counts x.

It appears that the predicted hind population was consistently lower than the observed counts and that two out of four counts were outside the 95% confidence interval for the true numbers of hinds. Conversely, the predicted stag population tended to be above the observed counts on average. To investigate this further, prediction intervals for counts instead of confidence intervals for predicted numbers were calculated (Table 5.9). All observed counts lie within the 95% prediction intervals for counts. The prediction intervals for counts were constructed by approximating the lower prediction limit by

$$C_l = \bar{\gamma}_{.,t} - \sqrt{(\gamma_{0.025n,t} - \bar{\gamma}_{.,t})^2 + 1.96^2\ \omega_t}$$

where $\bar{\gamma}_{.,t}$ is the average of all simulated deer numbers, $\gamma_{0.025n,t}$ is the 2.5 percentile of all simulated deer number and ω_t is the variance of observed counts. The upper prediction limit was calculated similarly.

Table 5.9. Counts and one year ahead predictions of population numbers as in figure 5.12. Also given are upper and lower 95% prediction limits for a count.
na = no count in that year

		Year (spring)								
		1987	1988	1989	1990	1991	1992	1993	1994	1995
STAGS	count	2729	na	na	na	na	4768	4780	5196	4077
	median	2716	3284	4064	4763	5379	5887	5250	5206	5109
	2.5%	1953	2174	2829	3232	3204	3081	4087	4067	3966
	97.5%	3473	4301	5267	6263	7180	7986	6426	6340	6198
HINDS	count	5489	na	na	na	na	5363	5299	4719	4029
	median	5477	5573	5775	5609	5420	5245	4604	4169	3954
	2.5%	3943	3342	2426	944	26	0	3520	3184	3046
	97.5%	7025	7102	7546	7662	7774	7978	5723	5211	4934
CALVES	count	2105	na	na	na	na	2273	2169	1299	1683
	median	2132	2627	2534	2411	2278	2121	1863	1831	1594
	2.5%	1235	1581	1403	844	170	0	1175	1187	1052
	97.5%	2992	3780	3590	3454	3409	3269	2556	2495	2170
TOTAL	count	10323	na	na	na	na	12404	12248	11214	9789
	median	10355	11501	12412	12803	13081	13214	11716	11240	10658
	2.5%	7868	8174	7600	5968	4464	3714	9214	8785	8370
	97.5%	12800	14476	15902	16959	17707	18567	14233	13661	12959

The predicted age distributions (average of simulation set) for yeld hinds, milk hinds and stags in 1995 were nearly identical for all three runs (Figure 5.13). Hence as far as predictions were concerned there did not seem to be much between run variation.

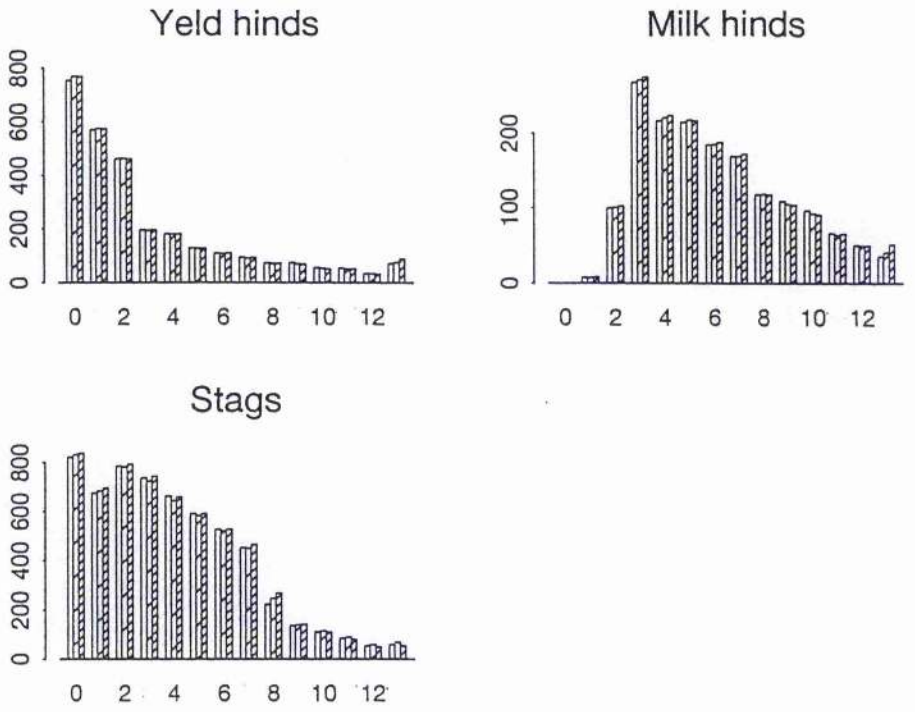


Figure 5.13. Predicted age distributions for 1995 when the population dynamics model was calibrated using data from red deer population in Caithness and Sutherland. The age group 13 contains all animals 13 years and older. Results of three repeat runs are shown.

Marginal prior and posterior parameter values were rather close for most parameters (Figure 5.14). Density estimates for marginal posterior values from all three runs differed slightly for some parameters though the three samples initially drawn from the prior parameter distributions showed similar marginal distributions. This means that although predictions were more or less consistent across runs, this was not necessarily true for marginal parameter estimates.

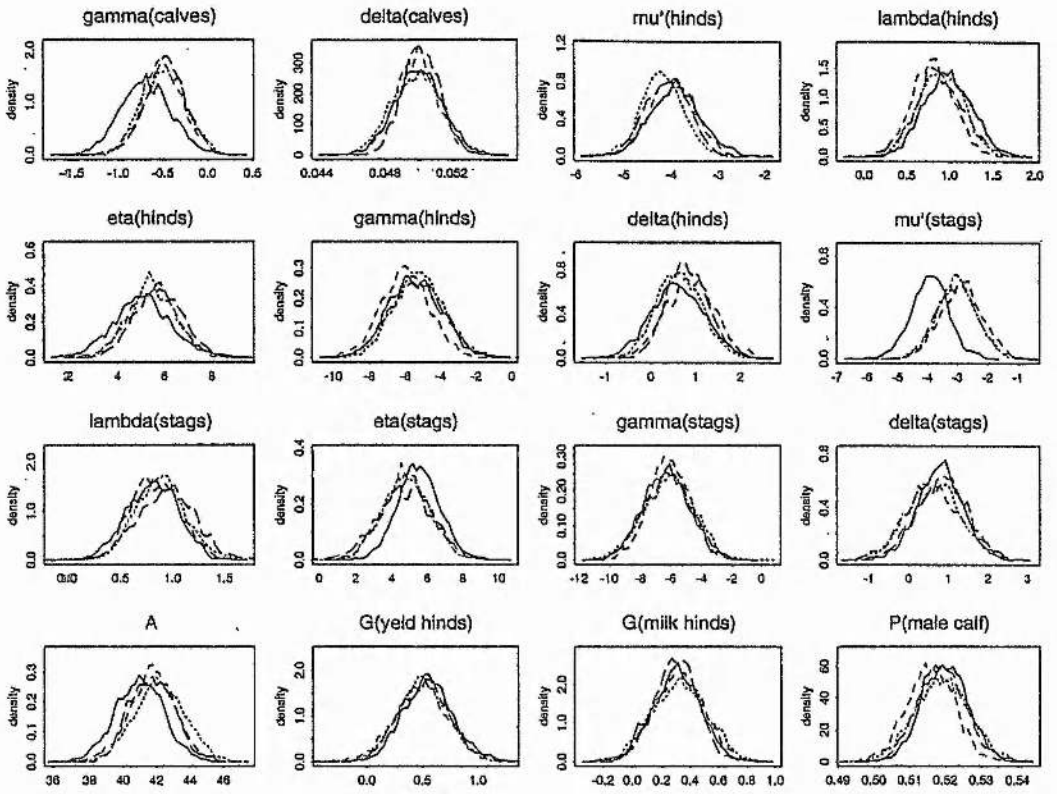


Figure 5.14. Density estimates for prior parameter values (solid line) and posterior parameter values (broken lines) obtained for the red deer population in Caithness and Sutherland after using 4 years of counts and running the updating algorithm three times.

Effects of updating simulated deer numbers

The calibration of the management model for the population in Caithness and Sutherland was repeated without the updating step of simulated deer numbers in the updating algorithm. The comparison between one year ahead predictions obtained with and without updating is given in Figure 5.15. Confidence intervals were slightly wider if no updating took place.

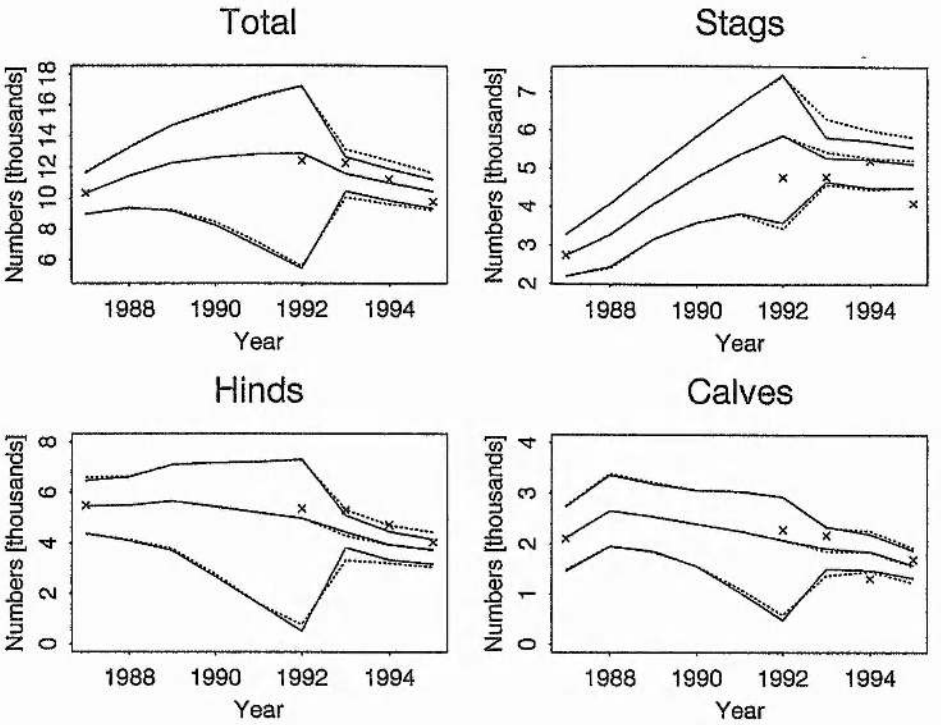


Figure 5.15. Calibrating the population dynamics model using data from red deer population in Caithness and Sutherland. One year ahead predictions of population numbers with 95% confidence intervals obtained without updating of simulated deer numbers in the updating algorithm (solid lines) in comparison to those obtained with updating (broken lines). Observed counts x.

Effects of classification bias in census counts

The possible bias in the classification of census counts was discussed in chapter 3. Discrepancies ranging from -2.6 to -12.1% for stags, from 14.5 to 25.8% for hinds and from -30 to 10% for calves had been found by Lowe (1971) when comparing reconstructed population numbers with counts. The results of a study investigating misclassification in census counts using two independent counts obtained on the same occasion were reported in section 3.2.1. Mean relative differences between the two counts were found to be -0.9% (0.16) for stags, -0.5% (0.1) for hinds and 4.4% (0.61)

for calves. Numbers in brackets indicate standard errors. All differences were smaller than found by Lowe (1971) but this approach did not quantify all sources of bias.

The possible effects of misclassified animals in census counts on the calibration of the population dynamics model were explored. Based on the extreme points of the misclassification rates for stags and calves found by Lowe (1971), three scenarios were investigated. In the first two scenarios stags were underreported by 3% and 12%. In the third scenario, stags were underreported by 3%, and calves by 20%. It was assumed that misclassified stags and calves had been classified as hinds. Hence, three new sets of count data were created by transferring the 'false' hinds into the stag and calf categories (Table 5.10). Cull numbers remained unchanged.

Table 5.10. "Count data" for the population in Caithness and Sutherland created for different scenarios of misclassification errors for stag and calf counts.

	Scenario 1 3% of stags counted as hinds			Scenario 2 12% of stags counted as hinds			Scenario 3 3% of stags and 20% of calves counted as hinds		
Year	Calves	Hinds	Stags	Calves	Hinds	Stags	Calves	Hinds	Stags
1987	2105	5405	2813	2105	5117	3101	2631	4878	2813
1992	2273	5216	4915	2273	4713	5418	2841	4647	4915
1993	2169	5151	4928	2169	4647	5432	2711	4609	4928
1994	1299	4558	5357	1299	4010	5905	1623	4234	5357
1995	1683	3903	4203	1683	3473	4633	2104	3482	4203

The density estimates of posterior parameter values obtained through the updating algorithm from each of the three created "count series" are shown in figure 5.16. The

results for the original count data are given for comparison (scenario 0). In general, posterior parameter values for scenario 1 were closest to the original results (scenario 0) for all parameters. Posterior values for scenario 3 showed the biggest difference. In particular, the posterior values of the intercept in the calf survival rate function, gamma(calves), showed a mode at around -0.8 whereas it was closer to -0.5 for scenario 0 and scenario 1. The values of scenario 2 were intermediate. The posterior calf survival rates were higher the larger the assumed counting bias (symbols in Figure 5.16a&b). The posterior parameter values indicating minimum stag mortality rates, mu'(stags), were largest in the case of scenario 3 which means that maximum stag survival was lowest (Figure 5.17a). The same trend was found for hind survival rates but with less pronounced differences (Figure 5.17b). The posterior values of the intercept of the fertility rate functions, A, were smaller for all three bias scenarios compared to the no bias case; the value of the posterior mode decreased from scenario 1 to scenario 3 which meant an increase in fertility rates in the same direction (Figure 5.18). These results are in line with the direction of the assumed counting bias. All three hypotheses assume that fewer hinds either produce the same number of calves (scenarios 1 and 2) or even more (scenario 3) than in the original counts (scenario 0). The posterior values for the slopes of the fertility rate functions for both yeld and milk hinds, G(yeld hinds) and G(milk hinds), had higher values for the modes in the case of hypothesis 3.The modes of the posterior density estimates for the probability that a calf is male were slightly larger for scenarios 2 and 3 compared to the other two scenarios which can be explained by the larger number of stags under those scenarios.

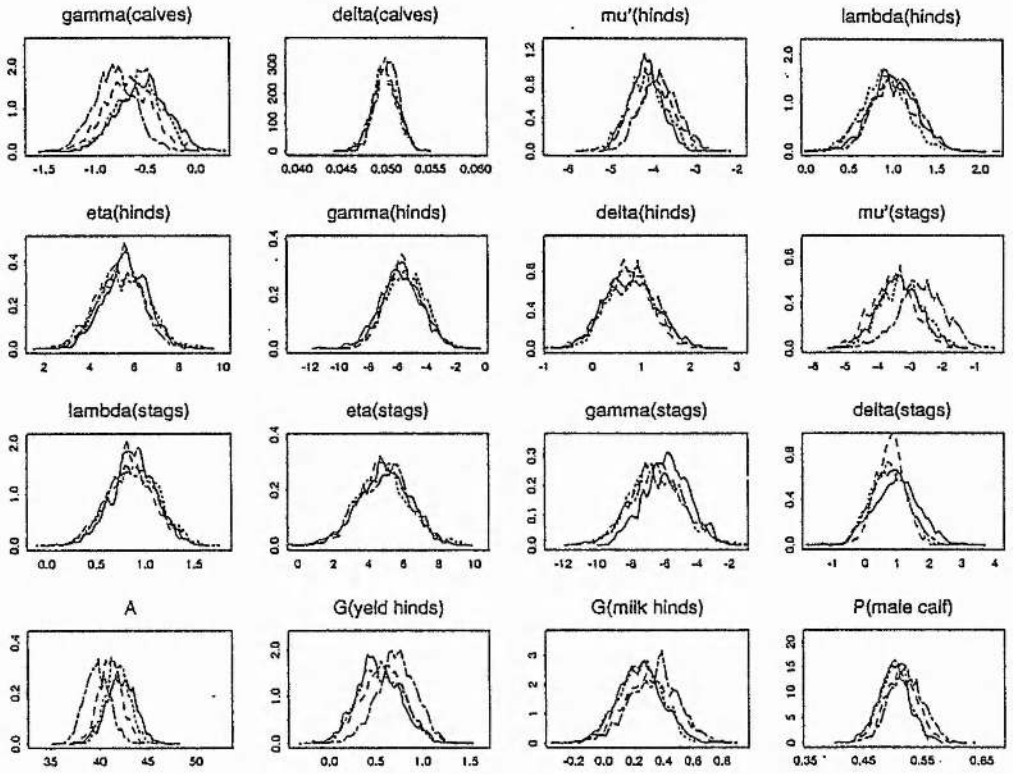


Figure 5.16. Density estimates for posterior parameter values obtained for the red deer population in Sutherland and Caithness after using 4 years of counts (solid lines) and for three data sets created from those counts assuming 3% of stags have been classified as hinds (dotted lines), 12% of stags have been classified as hinds (broken lines), and 3% of stags and 20% of calves have been classified as hinds (broken and dotted lines).

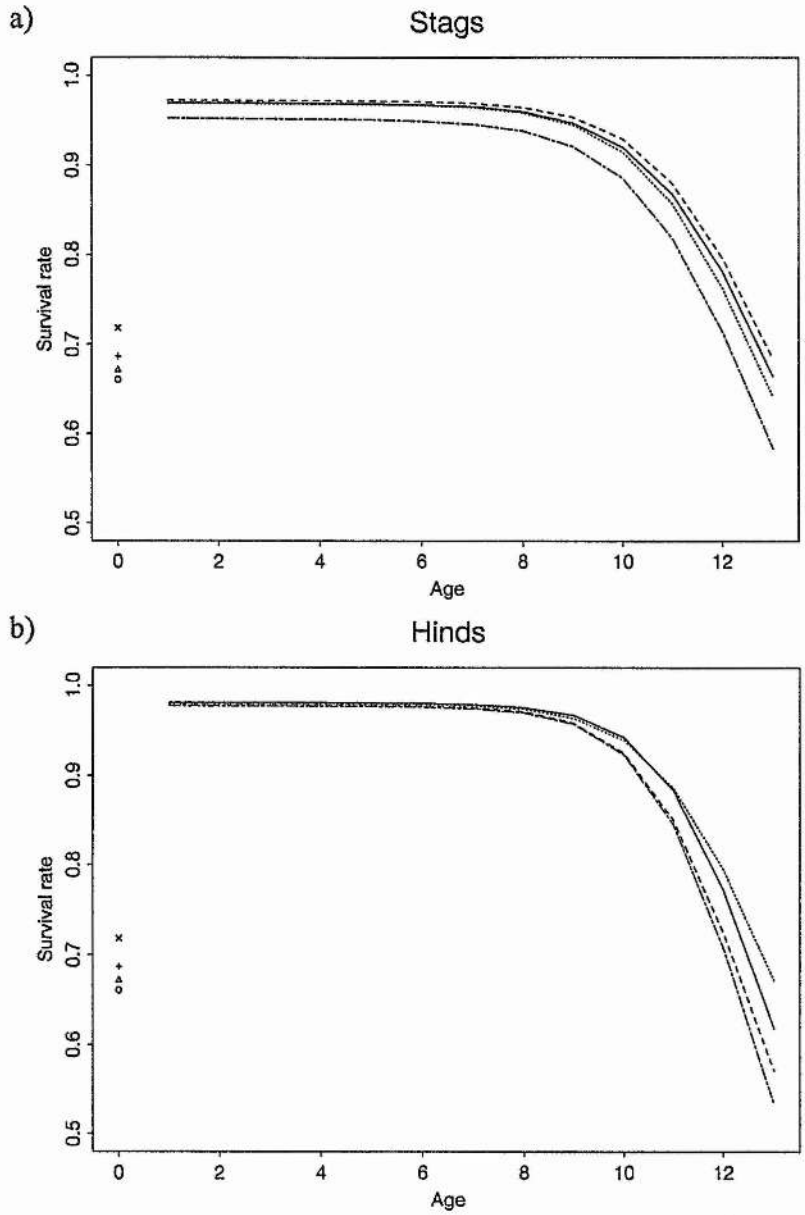


Figure 5.17a&b. Median posterior survival rates (at 15 deer per km^2) obtained for the red deer population in Sutherland and Caithness after using 4 years of counts (solid lines and circle for calves) and for three data sets created from those counts assuming 3% of stags have been classified as hinds (dotted lines and triangle for calves), 12% of stags have been classified as hinds (broken lines and plus sign for calves), and 3% of stags and 20% of calves have been classified as hinds (broken and dotted lines and cross for calves). Age group 13 contains all animals 13 years and older

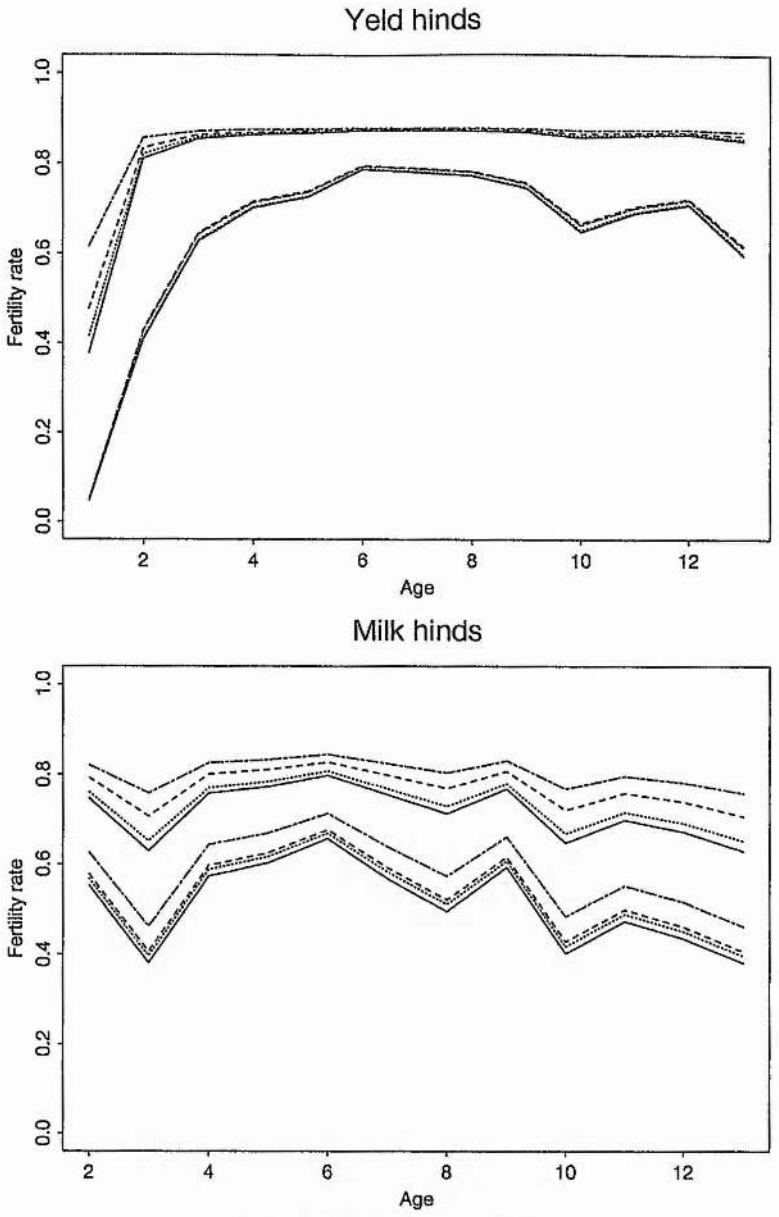


Figure 5.18. Median posterior fertility rates at 8.3 (upper curves) and 28.3 (lower curves) deer per km^2 obtained for the red deer population in Sutherland and Caithness after using 4 years of counts (solid lines) and for three data sets created from those counts assuming 3% of stags have been classified as hinds (dotted lines), 12% of stags have been classified as hinds (broken lines), and 3% of stags and 20% of calves have been classified as hinds (broken and dotted lines). Age group 13 contains all animals 13 years and older

The important question following from this study is whether bias in census counts might mislead deer managers by suggesting unsustainable culling levels. It will be

considered in chapter 6.

5.5.5 Case study 2

The updating algorithm was now applied to the red deer population on Islay, an island off the Scottish west coast. Between 1989 and 1997 the population was counted annually by the Deer Management Group for Islay with the exception of 1992 (S. Kennedy, pers. comm.). The numbers of stags, hinds and calves culled during these years were recorded. As no age specific culling rates were available it was assumed that different age classes were shot unselectively. The count in 1989 was used to create starting populations. A smoothing factor h=0.7 and a simulation set of size 2000 were used as before.

Calibration with narrow priors

The updating algorithm was run using the same parameter values and prior parameter distributions as for the previous example (see tables 5.2 and 5.3). These prior distributions are relatively narrow. Counts and annual one year ahead predictions of population numbers are given in Figure 5.19. Predicted deer numbers were lower than counts for hinds in most years but only in two years were counts outside the prediction confidence interval. Calf numbers agreed well. It was noticed that counts in some years were higher than expected based on the previous year's count and the cull. This might indicate that this population is actually not closed and could explain some of the discrepancies between model predictions and counts. Furthermore, it would appear that the model was consistently under-predicting hind counts which might indicate a

misclassification problem.

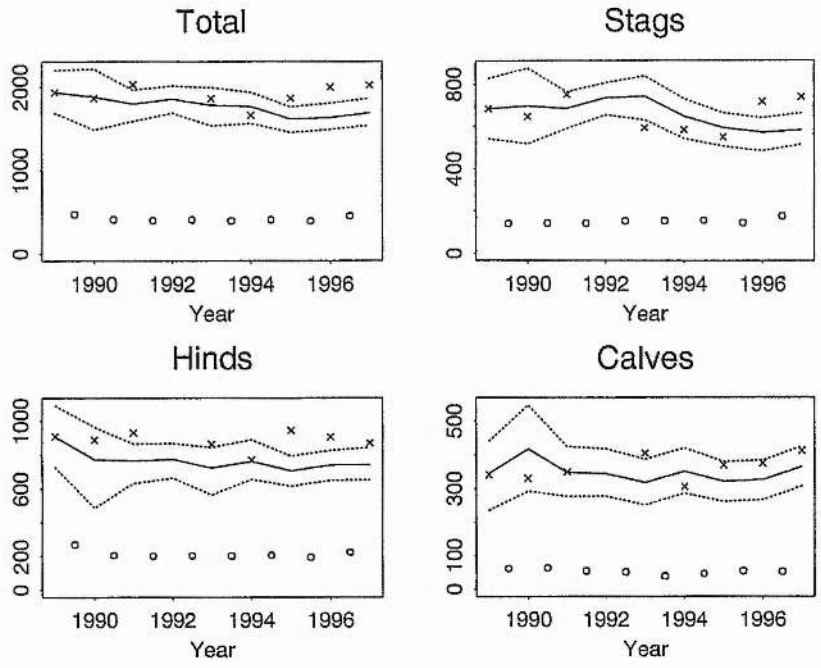


Figure 5.19. Calibrating the population dynamics model using data from red deer population on Islay. One year ahead predictions of population numbers with 95% confidence intervals. Observed counts (x) and culls (o).

Calibration with wide priors

To explore the effects the choice of prior distributions had on the calibration process, the updating algorithm was rerun using prior distributions containing little information for all parameters, with the exception of the parameter for the probability of a calf being male, whose prior was unchanged. Wide prior parameter distributions were obtained by setting the variance of all normal prior distributions to 100 and leaving mean values unchanged. The choice of the value for the variances is not important as long as it is large compared to the variances used for the 'informative' prior distributions. A value of 100 leads to wide distributions for all parameters even though they are on different

scales.

One year ahead predictions obtained starting from wide prior distributions became quite good after using two years of counts (Figure 5.20, dotted lines). However, confidence intervals were always wider than those obtained with narrow prior distributions.

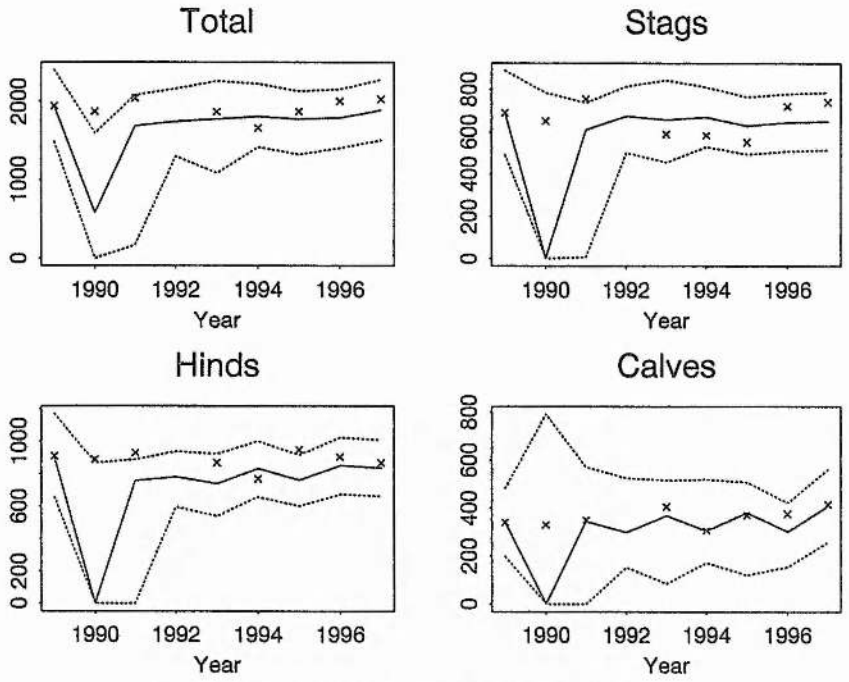


Figure 5.20. Calibrating the population dynamics model using data from red deer population on Islay. One year ahead predictions of population numbers with 95% confidence intervals. Observed counts (x) and culls (o). Results were obtained starting with narrow prior distributions (solid lines) and wide prior distributions (dotted lines).

The comparison of the wide prior and posterior parameter values is given in figure 5.21. It appeared that in this case the data did not carry much information on the parameters of the calf survival rate function, gamma(calves) and delta(calves) but the spread of most of the other parameter values had been reduced by the calibration process.

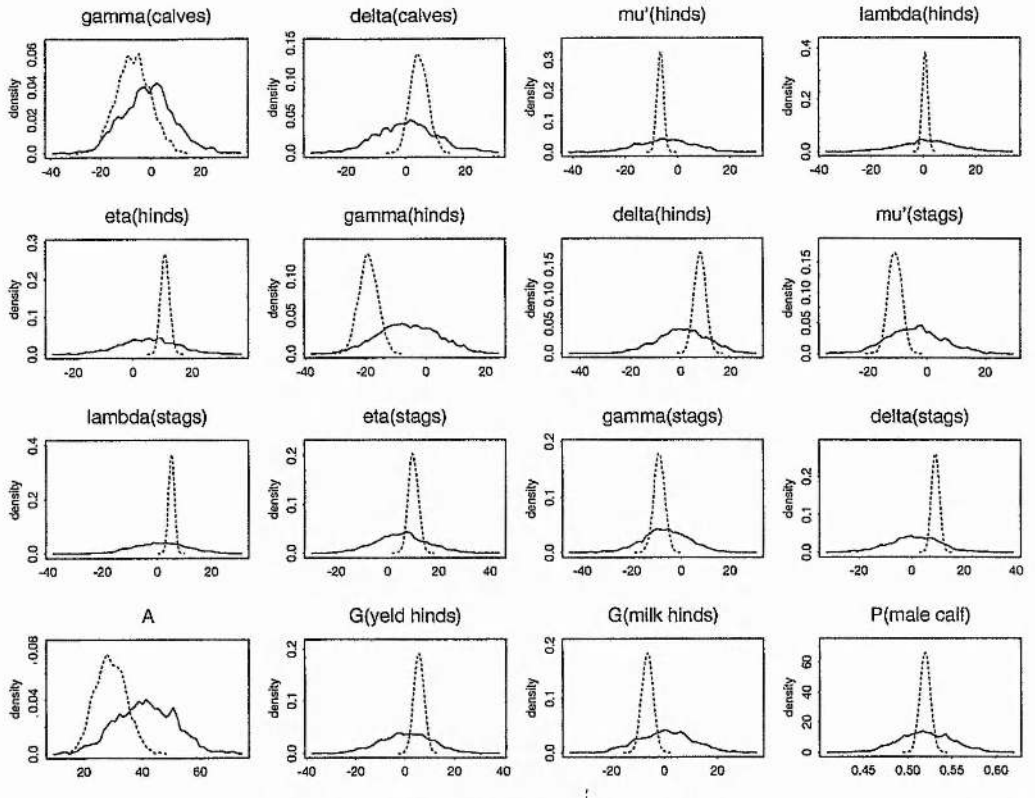


Figure 5.21. Density estimates for prior parameter values (solid line) and posterior parameter values (broken lines) obtained for the red deer population on Islay after using 7 years of counts and wide prior parameter distributions.

The plots of density estimates of posterior parameter values obtained starting from wide and narrow prior distributions showed that for most parameters, posterior values were not centred on the same values (Figure 5.22). In general, the spread of posterior parameter values was wider in the case of wide prior distributions. One noticeable exception is the parameter for the probability of a calf being male. Again this demonstrates the ability of the updating algorithm to identify a set of parameter values that were consistent with the counts in both cases though those parameter sets were not identical. A much larger simulation set would probably make predictions and posterior parameter values more consistent and less dependant on prior distributions.

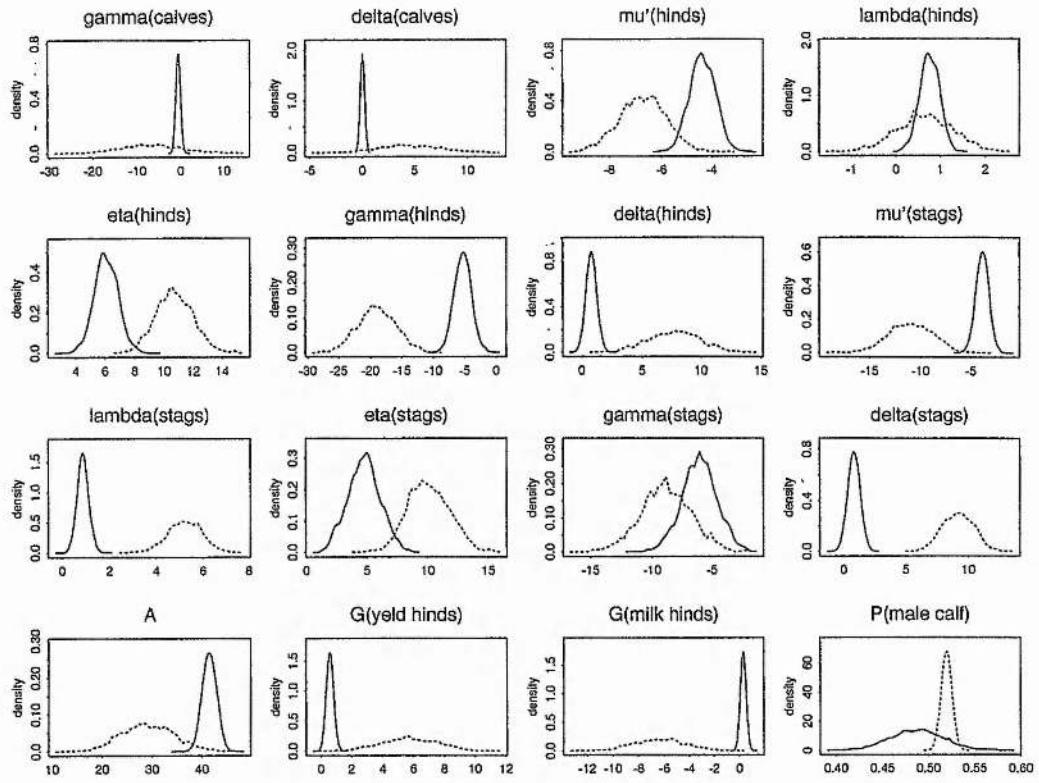


Figure 5.22. Density estimates for posterior parameter values obtained for the red deer population on Islay after using 7 years of counts. Results obtained using narrow (solid lines) and wide (dotted lines) prior parameter distributions.

Gain using updating algorithm

To demonstrate the effect the updating of parameter values had when starting from narrow prior distributions, the population was predicted three years into the future using first prior parameter values and then the posterior parameter values obtained above. It was assumed that no cull would take place in order to make differences more visible.

The predictions based on posterior parameter values were more precise than those based on prior parameter values (Figure 5.23). Furthermore, fewer stags and more

hinds were predicted when posterior parameter values were used which is in contrast to the results based on the priors.

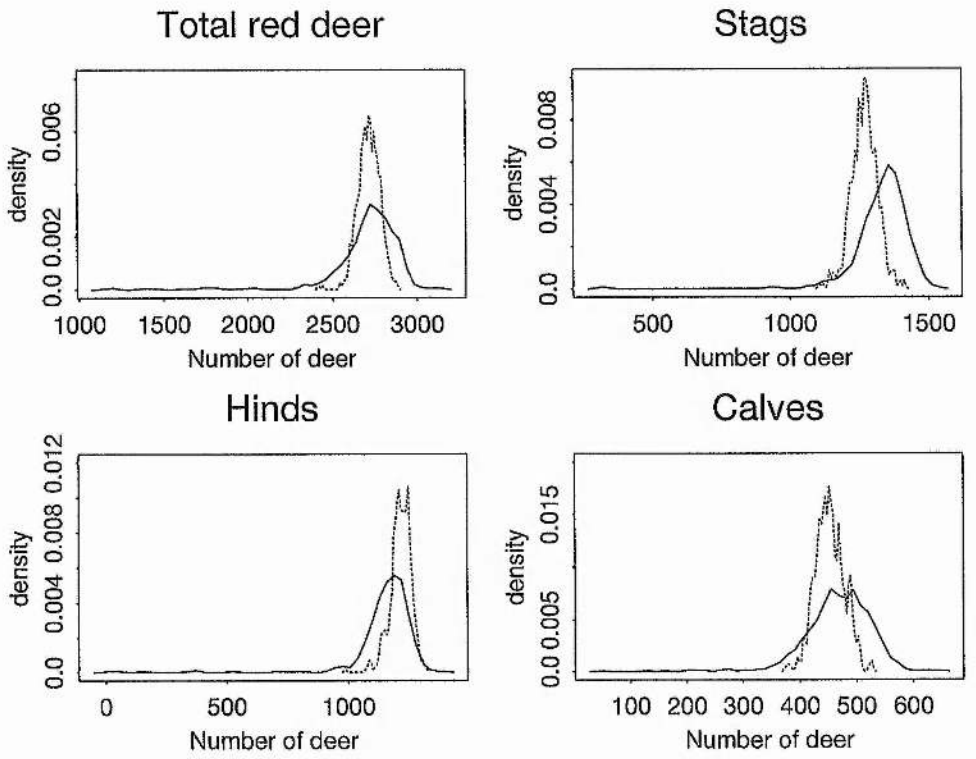


Figure 5.23. Density estimates of predicted deer numbers three years into the future using prior parameter values (solid line) and posterior parameter values (dashed line) obtained for the red deer population on Islay.

5.6 Discussion

5.6.1 Updating algorithm

General

A simulation-based algorithm was presented for sequentially estimating deer numbers as well as parameters in a population dynamics model using count and cull data. The updating algorithm is related to the method for drawing inference from implicit statistical models proposed by Diggle and Gratton (1984). Following Diggle and Gratton's notation, the population dynamics model (5.1) is an implicit statistical model for the counts in the observation equation (5.2). The full distribution of the counts $\boldsymbol{y}_t$ in (5.2), which can be derived from the distribution of animal numbers in different age-sex categories, $\boldsymbol{n}_t$, is quite complex. For this reason an approximate likelihood function was chosen. At any one time point, the likelihood function can be regarded as a kernel estimate of the true likelihood function based on one realization for each parameter set. Diggle and Gratton proposed kernel estimation of untractable likelihood functions based on multiple realizations for each parameter set. They then searched for the maximum of the likelihood to obtain parameter estimates. However, instead of searching for the maximum in the estimated multidimensional likelihood surface, the kernel estimates are used as weights to obtain a sample from the joint posterior parameter distribution.

A smoothing of the weighted bootstrap was introduced to make better use of the k simulation sets and the number of simulation sets was reduced to a few thousand

instead of several hundred thousand usually employed using the SIR algorithm (e.g. Raftery *et al.*, 1995). The smoothed bootstrap was set up in a way to preserve first and second order moments of joint posterior parameter distributions in line with Bayesian integration by simulation which is carried out without the smoothing step (Smith and Gelfand, 1992). However, the value of the smoothing factor affected the width of the confidence intervals of one year ahead predictions in an uncontrolled way which is unsatisfactory. Investigations would need to be carried out to see whether it would be possible to adjust the prediction confidence intervals and to further explore the relationship between the smoothing factor and the width of the prediction confidence intervals as well as the possible effects of other factors.

In the case study of red deer in Caithness and Sutherland the reduced number of simulation sets provided consistent estimates of deer numbers for repeated runs. Estimates of deer numbers as well as posterior model parameter values depended on prior distributions as the study using wide and narrow priors and data from Islay showed. The large parameter space and the confounding of some parameters added to the difficulty of obtaining consistent parameter estimates. Due to computational limitations it was however not possible to increase the number of simulation sets very much in order to explore whether consistent estimates which depended less on parameter prior distributions could be achieved. However, the gain achieved by using the updating algorithm was apparent for the predictions of red deer numbers which were usually quite good after a few counts had been used.

Borel's paradox

The Bayesian synthesis method has been developed for calibrating a deterministic population dynamics model for bowhead whales using prior information for both input and output parameters and combining this information via the model (Raftery *et al.*, 1995). It has been pointed out that the method suffers from Borel's paradox (Wolpert, 1995). Indeed, some combinations of parameters allowed by the marginal pre-model distributions of output parameters might be impossible given the pre-model distribution of input parameters and the deterministic population dynamics model and vice versa (Polacheck, 1995). Hence in this case Borel's paradox occurs because two incoherent pre-model distributions are specified for the same output parameters. Firstly, pre-model distributions are specified explicitly and secondly they are implied by pre-model distributions on other parameters. For example, consider the simple deterministic population model $N_t=N_0e^{rt}$ with pre-model distributions defined for N_0~$N(15,1)$ and N_5~$N(20,1)$. The growth rate is assumed to be constant, r =0.1. The pre-model distribution implied for N_5 is $N(24.7,2.72)$ which is not identical to the pre-model distribution specified explicitly and hence two incoherent pre-model distributions have been specified for N_5, which is an example of Borel's paradox. A consequence of Borel's paradox is that the post-model distributions for input and output parameters depend on the specific formulation of the model, e.g. transforming the model equation by taking the logarithm on both sides might lead to different post-model distributions (Wolpert, 1995).

Several routes to resolve the problems caused by Borel's paradox for the Bayesian Synthesis method have been suggested (e.g., Polacheck, 1995, Raftery *et al.*, 1996) and

a number of investigations have been carried out to establish the sensitivity of the method to Borel's paradox in the case of bowhead whale assessments (e.g., Givens and Bravington, 1995). To overcome Borel's paradox, Raftery et al. (1996) suggested geometric pooling of the two sets of pre-model distributions for output parameters, those pre-model distributions specified directly and those implied by the model and pre-model distributions for other parameters. The development of the Bayesian Synthesis Method continues.

The important question to answer is whether the updating algorithm is subject to Borel's paradox. For this investigation the example of the population dynamics model for red deer (5.7) is used. Independent prior distributions are defined for some of the model parameters (see table 5.3) and implied for all survival and recruitment rates. For example, the prior distribution for the survival rate for hinds of age one at a population density of 15 deer per km^2 is determined by

$$\phi_{1,0} = \{1-[\mu_0+(1-\mu_0)/(1+\exp(\eta_0-\lambda_0(-7)))]\}\ \{1/(1+\exp(\gamma_0+\delta_0(-3.3)))\} \quad (5.12)$$

where $\mu_0' \sim N(-3.89,0.3)$ with $\mu'_0 = \log(\mu_0/(1-\mu_0))$, $\eta_0 \sim N(-5.08,1.41)$, $\lambda_0 \sim N(0.99,0.08)$, $\gamma_0 \sim N(-5.47,2.1)$ and $\delta_0 \sim N(0.63,0.35)$. No explicit prior distribution is specified for $\phi_{1,0}$. Due to the functional form of (5.12), the implied prior distribution for $\phi_{1,0}$ will always be bounded by 0 and 1 whatever the independent prior distributions for μ_0', η_0, λ_0, γ_0 or δ_0. The same is true for all age specific survival and fertility rates. The specification of a particular prior distribution for one of the parameters in (5.12) (or in any of the other functions used for defining survival or fertility rates), does not imply anything about the values that other parameters in (5.12) may take. Thus, the priors specified cannot be incoherent.

Prior distributions are also specified for the number of animals $\mathbf{n}_0$ at time t=0 but not for any other years. Instead of using count observations to formulate prior distributions for the number animals in later years, the data are used in a likelihood approach. This is ordinary Bayesian analysis which does not suffer from Borel's paradox (Wolpert, 1995).

Extensions

The main feature of the updating algorithm is sequential parameter estimation where posterior parameter distributions at one time step become prior distributions for the following step. It would be possible to adapt the algorithm to follow time-varying parameters explicitly by assuming some functional form for this parameter change, for example a random walk. Furthermore, over longer periods of time one might expect demographic parameters to change due to changes in the habitat. If such changes over time are expected for red deer populations, it might be desirable to base future predictions on parameter values whose weights are more influenced by recent counts than by older counts. This means extending the updating algorithm to take account of the time span between subsequent counts used in the calibration process. A smooth function of the length of this time span could be defined and be used to reduce the weight the posterior distribution obtained at time t-k has in the estimation process at time t (Lambert, 1996).

An untested suggestion is made regarding the decoupling of the vector of simulated deer numbers and the corresponding simulated parameter values occurring in the smoothed bootstrap of parameters. Choosing a smoothing factor h as large as possible

reduces the degree of decoupling but in no way removes the problem. Theoretically the decoupling could be avoided if for each smoothed simulated parameter vector, the model would be run from time t=1 to the current time point in order to obtain the corresponding vector of simulated deer numbers. The question is then whether deer numbers should be updated or not.

The route that was chosen here to tackle the problem of calibrating a population dynamics model is based on the principle of sequential estimation which can easily integrate new information. There are other possibilities for calibrating the population dynamics model. Non-sequential Bayesian parameter estimation by simulation would be one possibility. Markov chain Monte Carlo methods as used in chapter 4 offer another approach, though they might be complicated to implement due to the large dimensionality of the state vector. For these methods the state vector would consist of all elements of $\boldsymbol{b}$ as well as $\boldsymbol{n}_t$ from t=1 to as many years as are modelled. For linear state space models with normally distributed noise in both the state and observation equations the problems due to the large dimensionality of the state space have been overcome (Carter and Kohn, 1994). However, the current population dynamics model for red deer is non-linear.

5.6.2 Population dynamics model for red deer management

A population dynamics model for red deer was proposed which includes density dependent effects as the main factors affecting survival and fertility rates. Modelling survival rates as a function of population density and fertility rates as a function of body weight and density distinguishes the proposed population dynamics model from

currently used red deer models (e.g., Forestry Commission model, Scottish Natural Heritage model) in addition to the fact that a stochastic model is used here and the other available models are deterministic.

Alternative formulations of the population dynamics model could be considered. For example, one could assume separate relationships between male and female calf survival and population density although no experimental evidence exists for such a difference (Guinness *et al.*, 1978). In this case, separate prior distributions would be specified for male and female calves for all parameters in (5.8). Given the nature of the count data which does not distinguish between male and female calves and which is used for calibrating the population dynamics model, proceeding along those lines would increase the variance of population estimates and also the number of confounded parameters. In the current formulation of the population dynamics model, the parameter representing the probability that the calf is male incorporates any differences which might occur between male and female calves. Thus the estimated probability that a calf is male may be biased by differences in survival or other factors such as classification bias in the counts.

The proposed population dynamics model has a rather large number of parameters making it very flexible, but also leads to the confounding of some parameters. The example with simulated data and the case studies illustrated this. A reduction of the dimension of the parameter space could be tried which could also reduce the problem of confounded parameters. Some of the parameters in the survival rate functions could be fixed, which was already done for two parameters in the fertility equation. The parameter representing the maximum survival rate, μ, might be a suitable candidate.

Any reduced adult survival would then be manifested as a reduction in the survival of older animals. Another route would be to look for a simpler population dynamics model. When considering the features of the 'best' population dynamics model, one has to bear in mind the purpose of the model and judge its merit in terms of how useful it is for achieving the stated aims.

In the next chapter, the red deer population in Caithness and Sutherland which was used in case study 1 will be studied further and the calibrated population dynamics model will be used to explore possible management strategies for this population.

Chapter 6 Application of the management model

6.1 Introduction

6.1.1 Decision support system

The population dynamics model for red deer together with the updating algorithm described in chapter 5 have been incorporated into a user-friendly decision support system called HillDeer. HillDeer was designed to support red deer management on the open hill in Scotland and includes several components: the population dynamics model presented here and models for vegetation growth, vegetation dynamics and grazing (Figure 6.1). The modules dealing with the habitat and grazing were developed by the Macaulay Land Use Research Institute.

The results of the questionnaire survey (chapter 2) were influential for the presentation of HillDeer and the options it incorporates. The following features were included in the population dynamics module of HillDeer:

- Calibration of the population dynamics model using the updating algorithm;
- Specification of starting population for projection into future; the options are count data from file, keyboard entry of numbers of stags, hinds and calves or continuation from previous run of model;
- Specification of sex and age specific culling strategies;
- Facility to identify a culling strategy to bring the hind population to a target level;
- Facility to specify extreme winter mortality for calf and adult animals in a specific year. All age specific mortality rates are rescaled so that mortality at age 4 (both sexes)

is equal to the specified adult mortality rate in that year.

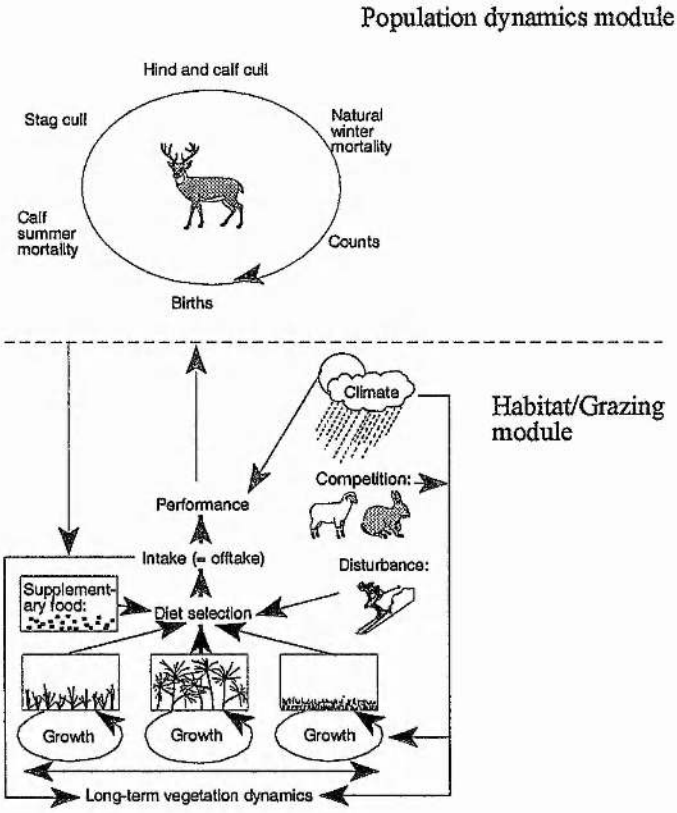


Figure 6.1. Modules of HillDeer, a decision support system for the management of red deer on the open hill in Scotland.

The habitat/grazing module of HillDeer consists of several submodels (Partridge, 1997a, 1997b & 1997c). The grazing by red deer and also sheep and rabbits (if any) on up to six different open-hill vegetation types is modelled. There are three grassland vegetation types (bents and fescues, mat grass and purple moor grass) and three heathland types (dry heath, wet heath and blanket bog). Woodland is not considered. The growth and competition of the different vegetation types throughout the year are modelled. As a result of the competition, the areas of the different vegetation types can

change over time (vegetation dynamics). Plant growth is affected by rainfall, day length and grazing pressure. The grazing model considers the change of body weights of the red deer over time as they feed and grow (or lose weight) according to the food available to them. Energetic requirements are influenced by wind speed and temperature and also by gestation and lactation for hinds and the rut for stags. Some of the red deer may have access to winter supplementary feeds and disturbance by humans may affect where they choose to feed.

HillDeer has three working modes. The population dynamics module and the habitat/grazing module can either be run individually or together. If the population dynamics module is run on its own, changes in red deer performance due to climatic or vegetation changes are not taken into account unless the user specifies a specific mortality rate using the severe winter option. However, changes in population density are assumed to affect survival and fertility of red deer. If the habitat/grazing module is run on its own, the age and sex structure as well as the number of red deer remain constant over time. If both modules are run together, the population dynamics module provides current estimates of red deer numbers at various times of the year and the habitat/grazing module returns estimates of current body weights in autumn.

Here the population dynamics module of HillDeer was used on its own to explore management options and their consequences for the red deer population in Caithness and Sutherland which was already used in chapter 5. These investigations are exploratory in nature and demonstrate the use of the management model rather than provide definitive answers regarding the best management of the population. The effects of bias in census counts on posterior parameter values was investigated for this

population in section 5.5.4. Here the impact bias in census counts might have on management is explored.

6.1.2 Study population

The study population in Caithness and Sutherland (Figure 6.2) dwells in an area of about 919 km^2 (Clutton-Brock and Albon, 1989). The habitat is flat and open with a few enclosed conifer plantations. The red deer population is seen to consist of three sub groups with a seasonal movement towards the coast in winter. The three main land uses are red deer, sheep and grouse (R. McNicol, pers. comm.).

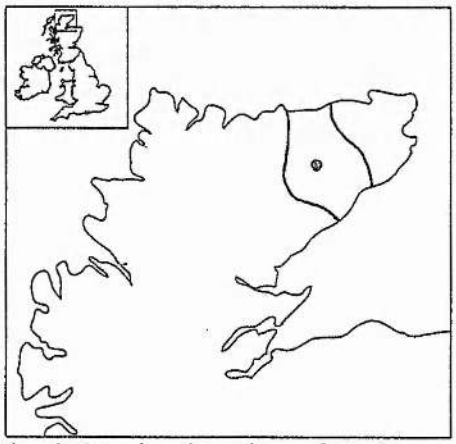


Figure 6.2. Map of Scotland showing location of study population in Caithness and Sutherland.

This red deer population has been managed cooperatively by the Northern Deer Management Group since about 1987 and comprises 25 estates. The following information has kindly been provided by R. McNicol, secretary of the Northern Deer Management Group. The Deer Management Group has two meetings a year. The stalkers meet in April after the annual count (which takes place in February/March) to discuss deer numbers and culling strategies. Estate owners meet in September for

financial discussions, common venison marketing and discussions on poaching problems. The main management aims are sporting culls with both stag and hind shooting being let out to paying clients. Cull sizes are discussed every year by the stalkers. The DMG makes recommendations to the individual estates but the final decision rests with the estate. The size of the stag cull is determined by demand and the attempt to keep numbers stable. The hind cull is determined annually in relation to producing the required stag cull. Stags are shot from about maturity (4-5 years), though younger stags are shot if they appear to be in poor health. For hinds, the strategy depends on the population size. If numbers are too high, all age classes are shot irrespective of whether they have a calf at foot. If numbers are about right, mainly old yeld hinds and ill animals are targeted. Few milk hinds with their calves are taken in this case. In addition to the annual cull, deer are shot as marauders, mainly in the north and about 50 deer are killed annually by trains. Poaching poses few problems. The state of the habitat currently plays no role in red deer management. However, no natural tree regeneration seems to take place currently indicating that there might be overgrazing. The numbers counted and shot in recent years are given in Figure 6.3.

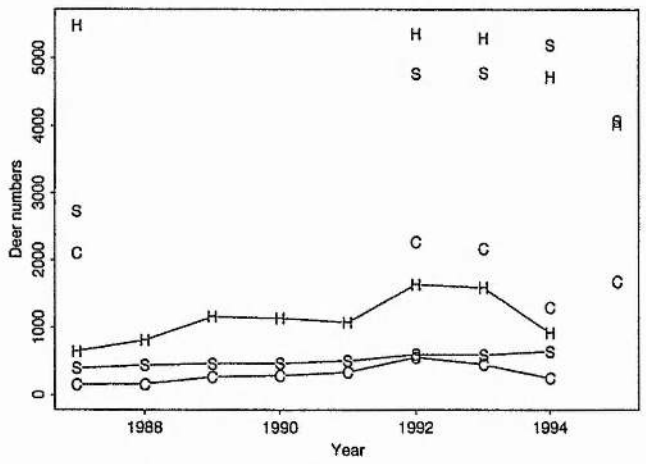


Figure 6.3. Count (symbols) and cull data (lines) for red deer in Northern Deer Management Group. S=stags, H=hinds, C=calves.

6.2 Management objectives

6.2.1 Description

The calibrated population dynamics model of chapter 5 was used to explore the effects of different culling strategies and identify strategies for maintaining the stag cull taken in 1994. For age-selective culling, the following definitions were used. Young animals are aged one to four years, mature animals five to ten and old animals are 11 years or older. Here, yeld hinds are all hinds without a calf at foot and are older than one year.

Two different management objectives were defined. Management objective MO1 was to keep the population stable and achieve a sustainable stag cull at least as high as the 640 stags culled in 1994. The question of how big a population would be needed for a sustainable stag cull of about 600 animals and what kind of hind cull that would require was investigated. Management objective MO2 was to find a population level and culling strategy that would achieve this.

Table 6.1. Management objectives for study population in Caithness and Sutherland.

Objective	Stag strategy	Hind strategy
MO1	stag cull of about 600 stags	hind cull that keeps total population stable at about 10,000 (1995 level)
MO2	find stag population size for a annual stag cull of about 600	find hind population size and hind cull that sustains stag cull

6.2.2 Culling strategies for management objectives and projection results

All culling strategies were kept constant over a thirty year period. A number of culling strategies were explored for both management objectives. Predictions for management objectives MO1 started from the count in 1995 and with the age distributions obtained from the calibration and might not correspond to the truth (Figure 6.4). However, culled animals were not aged in the past and therefore the true age structure of this population is unknown.

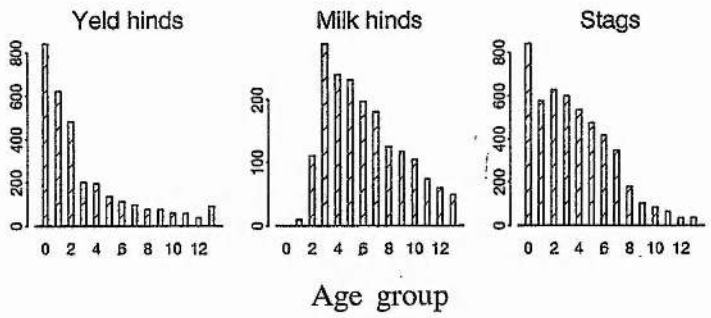


Figure 6.4. Average predicted age distribution of the study population in 1995 based on calibration of the population dynamics model (see chapter 5). Age group 13 contains all animals 13 years and older.

Management objective MO1 was to find a culling strategy that would keep the population constant and still give a large stag cull. One strategy achieving this goal is given in table 6.2. Note that this strategy is not the only one that would fulfil the requirements of management objective MO1.

Table 6.2. Culling strategy for management objective MO1.

Stag culling strategy	Hind culling strategy
10% of young animals	20% of young yeld hinds
50% of mature animals	20% of mature yeld hinds
90% of old animals	90% of old yeld hinds
	3% of all ages of milk hinds
	6% of calves shot

This culling strategy yields sustainable culls and seems to lead to a stable population in the long run (Figure 6.5). Initially, average total deer numbers decreased slightly due to a decrease in stag numbers. This was caused by a predicted reduction in the number of mature and old stags.

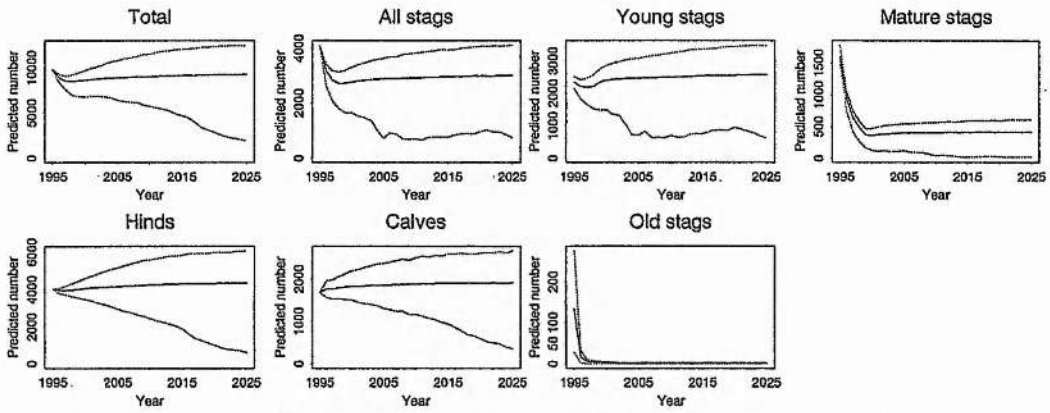


Figure 6.5. Predicted deer numbers using strategy for management objective MO1. Figures show mean predictions with 95% confidence intervals.

The long term predicted total cull was about 1700 deer of which 760 were stags, 800 were hinds and 140 were calves (Figure 6.6). About half the culled stags would be young animals and the other half mature where most of the mature animals would be five or six years old.

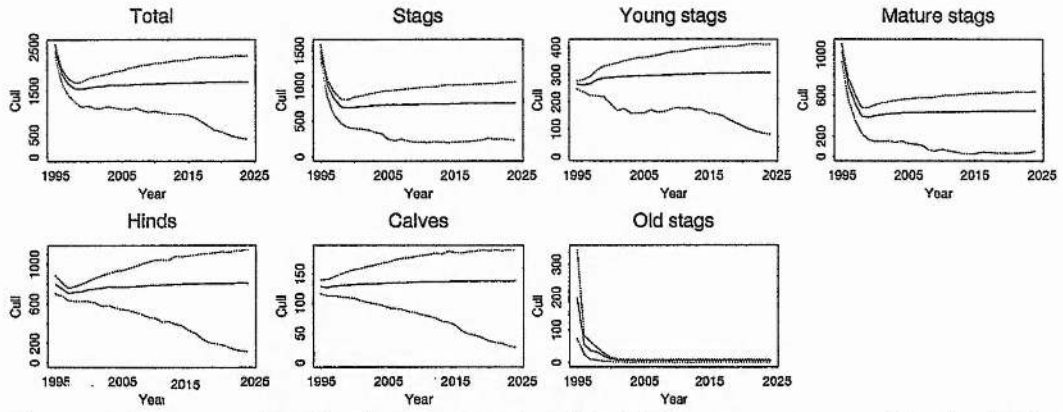


Figure 6.6. Predicted cull using strategy in table 6.2 for management objective MO1. Figures show mean predictions with 95% confidence intervals (dotted lines).

To achieve management objective MO2 a population level was sought that would sustain a stag cull of about 600 animals. It was found that a total population of about 8300 deer could give a stag cull of just under 600 animals using the culling strategy given in table 6.3.

Table 6.3. Population size and culling strategy for management objective MO2.

Population size	Stag culling strategy	Hind culling strategy
8300 total	5% of young animals	21% of young yeld hinds
3100 stags	40% of mature animals	21% of mature yeld hinds
3500 hinds	90% of old animals	90% of old yeld hinds
		4% of all ages of milk hinds
		4% of calves

These results were obtained by starting from different population levels and varying the culling strategy. Starting from a population with 2900 stags, 3000 hinds and 1400 calves and applying the culling strategy of table 6.3 a nearly stable population was

predicted (Figure 6.7a). The average predicted population size was around 8300 red deer with 3100 stags and 3500 hinds which would be regarded as the kind of population level needed to satisfy objective MO2. The predicted average stag cull for this strategy was just under 600 animals with two thirds being mature animals. For hinds, the average predicted cull is close to 700 whereas it was only about 80 for calves.

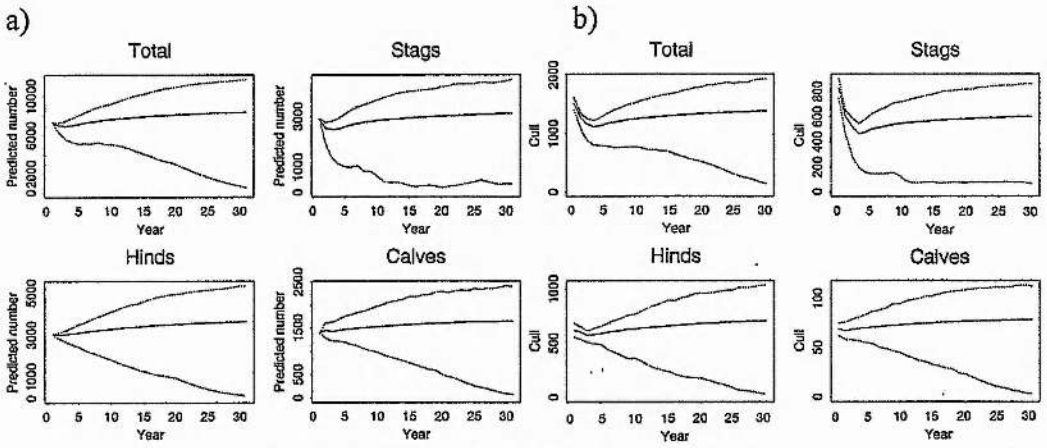


Figure 6.7. Predictions for strategy suitable for management objective MO2. Figures show mean predictions with 95% confidence intervals (dotted lines).
a) Predicted numbers; b) Predicted cull.

6.3 Impact of classification error in counts on management

The effects classification error in census counts might have on posterior parameter values when the updating algorithm is used has been looked at for this study population (section 5.5.4). The question whether classification bias in census counts would compromise the choice of culling strategies is of interest here. The magnitude of any classification bias is unknown in general. The important point is therefore whether a given culling strategy will have the intended effect if classification bias is present but ignored. A small case study was carried out to explore the possible implications. In

chapter 5, four scenarios about the classification bias were considered. The same cases are used here: 1. no bias in census counts (scenario 0); 2. minus 3% bias in stag counts in which 3% of stags have been recorded as hinds (scenario 1); 3. minus 12% bias in stag counts (12% of stags recorded as hinds) (scenario 2) and 4. minus 3% bias in stag counts and minus 20% bias in calf counts, in which 3% of stags and 20% of calves have been counted as hinds (scenario 3).

The chosen management objective was to keep the population stable, in particular the hind population. A culling strategy which would approximately achieve this aim was identified for the case with no counting bias, starting the projections from the population counts in 1995 and using the corresponding posterior parameter values (Table 6.4).

Table 6.4. Annual culling rates in percent for keeping population in Caithness and Sutherland roughly stable when assuming no bias in census counts.

Age group	Stags	Yeld hinds	Milk hinds
calves	4.4	4.4	-
young	2.0	22.2	4.4
mature	40.0	22.2	4.4
old	90.0	22.2	4.4

The same culling rates were applied to the three scenarios which assumed various degrees of counting bias. Median predicted population estimates for all scenarios of counting bias are presented in figure 6.8. In most years, the median predicted population estimates for each scenario lie within the 95% confidence intervals for the

estimates of the other scenarios.

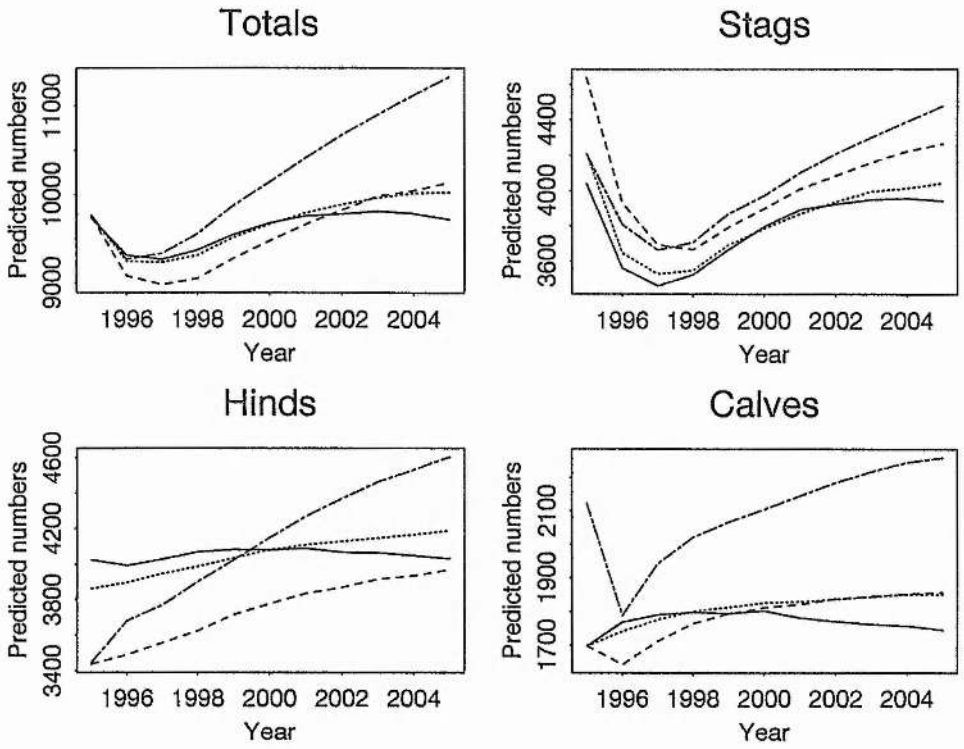


Figure 6.8. Median predicted population size of red deer population in Sutherland and Caithness when applying culling rates of table 6.4. The results are based on calibrating the model using the original counts (solid lines) and three data sets created from those counts assuming -3% bias in stag counts (dotted lines), -12% bias in stag counts (broken lines) and -3% bias in stag counts as well as -20% bias in calf counts (broken and dotted lines).

The hind predictions obtained assuming no counting bias were about stable over the ten year period. Stag numbers decreased initially due to the heavy culling of mature animals and stabilised after about six years (2001). The total population estimates followed the same trend. The predicted total population numbers obtained for the three scenarios of counting bias did not stabilise within the ten year period. However, the predicted total population numbers were close to stable for the cases of bias in stag counts only (scenarios 1 and 2). The larger the assumed bias in stag counts, i.e. more stags have been counted as hinds, the greater this rate of increase in total population numbers

which was due to increases in both hind and stag numbers. The population estimates for scenario 3 did not stabilise at any point and showed a 16% increase over ten years.

Nevertheless, by applying culling rates obtained from using counts which were assumed to be unbiased it would be possible to nearly stabilise populations over a ten year period which had different underlying compositions of stags, hinds and calves (in two out of the three cases considered). In the example presented, differences in the median of predicted total deer numbers became most noticeable after more than six years. If a population was counted annually, such discrepancies would be picked up and appropriate action could be taken, for example by increasing culling rates. Hence in the two cases of classification bias only for stag counts (scenarios 1 and 2) ignoring this bias for the calibration of the population dynamics model would still lead to a culling strategy that could keep the true underlying populations about stable.

6.4 Discussion

The 95% confidence intervals for all future predictions increase with time and get rather large after a few years. The important question arising from these rather large confidence intervals is how they affect the practical usability of the management model. In practice, decisions on culling strategies are revised annually and long term predictions should serve as guidelines on what kind of strategy would achieve a certain objective. However, it is important that the current population size is assessed regularly. Counting every 2-3 years might be sufficient in average years. However, after a severe winter, a count is recommended. Each time a count is available, the model is calibrated. Running the updated model again can then help to decide whether a change

in strategy is required in order to pursue the original objectives or whether the culling strategy of the previous year(s) should be continued. Hence, due to this frequent feedback between what is really happening and what the model predicts, the uncertainty in model predictions for long term predictions is not problematic.

The question of the causes for the rather large long term prediction variance and what could be done to improve them is considered. In order to distinguish between uncertainty due to parameter uncertainty and stochastic effects, the predictions for the strategy for MO1 were repeated using a deterministic version of the population model dynamics model. The results were rather similar to what was obtained before with the stochastic model (Figure 6.9). Hence the uncertainty in predictions seems to be due to parameter uncertainty.

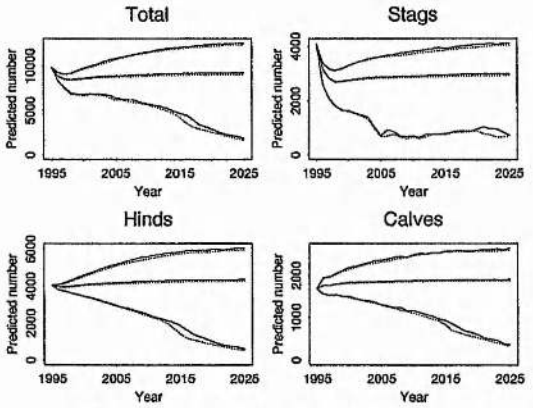


Figure 6.9. Comparing predictions for strategy suitable for management objective MO1 using stochastic (solid line) and deterministic (broken line) population dynamics models. Figures show mean predictions with 95% confidence intervals.

Using the two management objectives it was demonstrated how the model can help to identify sustainable culling strategies. The culling strategies that were found to achieve both management objectives (MO1 and MO2) were similar for all animal groups apart

from young stags because both were intended to keep the population stable at a certain level with the additional specification for MO2 to identify this level conditional on achieving a certain stag cull. The deer densities corresponding to the stable populations of MO1 and MO2 are about 10 and 9 deer per km^2, a difference in deer density which does not result in much difference in survival rates. However, the important point to note is that the culling level of young stags for MO2 is half that for MO1 and a bit smaller for mature stags, which means that fewer hinds are required under MO2 to achieve about the same cull (400) of mature stags.

All these results are based on a particular age distribution in 1995 which was obtained by assuming unselective culling for the calibration of the model. The predictions in the first couple of years depend very much on this assumption whereas in later years the effects of certain culling strategies will have fed through all age classes and this dependency no longer holds. Hence, if culling was not unselective, the predicted age distributions in the first few years will not correspond to what might happen to the population in reality. This point emphasises the importance of ageing culled animals in order to make informed decisions about future culling policies.

Having found that age specific culling was more efficient in terms of the number of stags that could be culled from the study population, the question poses itself whether it is actually feasible to implement such strategies in practice. It is assumed that it would be possible to some extent to distinguish very young animals from old animals whereas this might be more difficult for intermediate age groups. However, if culled animals are aged (including out of season culls), the model can be updated and the culling strategy changed to reflect the culling strategy that was implemented rather than the one that

was intended. As stressed before, frequent (ideally annual) assessment of culling strategies is essential.

A simple case study was carried out to investigate the impact of classification bias in census counts on the effects of a certain culling strategy. For the three scenarios considered, in two cases did the culling strategy that about stabilised the population within a ten year period and which was identified by ignoring any classification bias also nearly stabilise those populations. The approach taken here could be used to check the robustness of any culling strategies in practice when the true composition of a population and the magnitude of any classification bias are unknown.

The results presented here demonstrate the kind of questions that can be investigated using the management model for red deer. Looking at the effects of a number of different culling strategies can give insight into the likely effects of possible management options.

Chapter 7 Discussion and conclusions

7.1 Estimating red deer abundance

The feasibility of aerial line transect methods for estimating red deer numbers on the open hill in Scotland was demonstrated (chapter 3). It was shown that aerial line transects allow large areas to be surveyed more efficiently than is possible using the traditional census method given the habitat is suitable for its application. Based on the trial study a number of recommendations were made on how the aerial line transect method could be improved. In particular, the use of a Global Positioning System for following the transect lines was proposed and the testing of the software written by Anthony and Stehn (1994) was recommended. For speeding up the survey it was suggested that animal groups only up to a distance of 50 m on either side of the transect line should be classified. A study should be carried out to estimate the average increase in surveying speed achieved by implementing this recommendation. The use of a thermal imager for improving detection of animals has been found successful in forest habitats (Gill *et al.*, 1997) and should be tested in aerial surveys of open hill habitat. It was suggested that the improved aerial line transect method would reduce the coefficient of variation from 25% to at most 10%. A study should be carried out to ensure that this is the case. Ideally, this study should cover a much larger area than was possible in the study presented here. The area should at least be the size of a full counting block, and ideally should comprise several counting blocks. This would also test the feasibility of the new counting scheme suggested in chapter 4. Under this counting scheme, the red deer range in Scotland would be divided into three to five regions which could be surveyed by aerial line transects more often than is currently possible using census

methods.

The Markov chain Monte Carlo method used in chapter 4 provided estimates of red deer population trends on a Scotland wide level using historic census counts and cull information. However, convergence problems cast doubt on the reliability of deer density estimates. Nevertheless, the use of a random effects model with random year and region effects made it possible to include counting blocks which had only been counted once, which is an advantage over regression techniques previously used by Clutton-Brock and Albon (1989) for estimating deer densities. The aerial line transect method could also be used to provide the population abundance estimates needed for the Markov chain Monte Carlo estimation method. If the aerial line transect method is used, the abundance of red deer in individual counting blocks or larger regions could be estimated more frequently, since each survey is less expensive. As a consequence, better estimates of the total number of deer might be achieved using Markov chain Monte Carlo methods.

A counting scheme for individual counting blocks based on the ideas of optimal resource allocation and reduction of the variance of total deer estimates was proposed. This approach was somewhat simplistic and more sophisticated studies could be carried out to investigate optimal counting schemes within the framework of Markov chain Monte Carlo estimation methods.

The 'best' counting scheme and the scale of abundance surveys depend foremost on the use that is to be made of the abundance estimates. General monitoring of deer numbers does not require the same geographic resolution as the management of individual red deer populations.

7.2 Management model

An age and sex structured population dynamics model was developed for assisting the management of individual red deer populations (chapter 5). In the past, population dynamics models used for management have only been parameterised for specific populations as the required detailed information on demographic processes is not readily available for many red deer populations (Beddington and Taylor, 1973; Beddington, 1974; Clutton-Brock and Lonergan, 1994; Buckland *et al.*, 1996).

An updating algorithm was developed for combining detailed demographic information from a few well studied populations with counts and cull data from the local population of interest. The updating algorithm selects a set of plausible parameter values for the local population which can then be used to explore future culling strategies. The questionnaire survey of holdings (chapter 2) showed that cull and count information was collected routinely by most holdings and could be relied on as input for a management model.

Using the calibrated management model (chapter 6) it was shown how culling strategies to achieve a certain management objective can be identified. It is noted that the ageing of culled animals would allow a better picture of the age structure of a population to be built up, which in turn would allow more reliable predictions of the development of a population in the short term. Hence one would hope for more ageing of culled animals in the future.

Concern has been raised regarding the misclassification of census counts (Lowe, 1971; Clutton-Brock and Albon, 1989 & 1991). A study was carried out to assess the possible magnitude of this classification problem (section 3.2.2). Rather small relative classification errors were found when comparing the counts of a counter with those of an independent verifier. The 95% confidence intervals for the classification errors found were -1.2 to -0.5% for stags, -0.7 to -0.3% for hinds and 3.2 to 5.6% for calves. These results were based on the assumption that the verifier's counts were correct. However, it is conceivable that the counts of both the verifier and the counter were subject to misclassification of unknown magnitude. In any case, this study did not quantify any variation in census counts due to missing groups, counting groups more than once or movement of groups between counting blocks. The estimated classification errors were much smaller than the discrepancies presented by Lowe (1971). Lowe's results were obtained by comparing reconstructed deer numbers with Deer Commission census counts on Rum.

To explore the likely effects of misclassification in census counts on model calibration and the identification of a sustainable culling strategy, some investigations were carried out for a study population (section 5.5.4 and section 6.3). In two of the three cases considered, the culling strategy that about stabilised the population within a ten year period, ignoring any classification error, also nearly stabilised those populations. It was suggested that an approach which consists in varying the classification of census counts used for the calibration could be used to check the robustness of any culling strategies identified with the management model when the true composition of the population and the magnitude of any classification error are unknown.

Before classification bias in census counts can formarly be included in the updating algorithm, more studies need to be carried out to quantify the classification bias and estimate a table of confusion probabilities, i.e. the probability of confusing a stag with a hind and conversely of confusing a hind with a stag and similarly for confusions between stags and calves and hinds and calves. Carrying out a study which would allow the estimation of these confusion probabilities is not straightforward. Neither the verification design used in section 3.2.2 nor comparison of reconstructed populations and counts can be used. Counts of a population with individually marked animals could provide the necessary information. In the current formulation of the updating algorithm, the counting error is assumed to be symmetrical and independent for each of the three categories stags, hinds and calves. This assumption might be modified by using the estimated confusion table.

The confidence intervals of one year ahead predictions of deer numbers were estimated as the percentile points of all simulation set members in the updating algorithm. The width of those confidence intervals depended on the smoothing factor used in the smoothed bootstrap of model parameters. The value of the smoothing factor was chosen in order to encompass between run variation which was due to the relatively small size of the simulation set. However, the choice of the smoothing factor was somewhat *ad hoc* and it would be important to formally establish the relationship between the smoothing factor and the prediction confidence intervals in order to attempt a correction if desired. The effect of the size of the simulation set should be investigated in that context as well.

A number of further developments of the updating algorithm could be envisaged. The

updating algorithm could be extended to downweight past information by modelling the time span between successive counts used in the calibration process (Lambert, 1996). Currently the observation error (counting error) is a linear function of the counts assuming a constant coefficient of variation for this counting error. The counting error could also be formulated as a function of the state, which is the number of deer in a given category in a given year. In this case a modified version of the generalised Kalman filter could be used for the updating of simulated deer numbers (Zenwirth, 1988; Harvey, 1989).

One of the problems that had to be dealt with by the updating algorithm was the linking between the population dynamics model on one scale of resolution and the data collected at a lower resolution. The result of this was the confounding of some parameters in the population dynamics model. Several suggestions were made for dealing with this problem of confounded parameters. Some of the parameters could be fixed, or a simpler population dynamics model defined, for example by excluding density dependence of survival rates. Future work could look at the problem the other way round. This means specifying the population dynamics model on the scale of resolution of the observations and linking it to an age-structured model designed for management purposes. Within the current framework such a population dynamics model could be achieved by assuming separate constant survival rates for hinds of all ages and status, stags of all ages and calves of both sexes respectively. For the fertility rate there would be no distinction between yeld and milk hinds and different age groups. Alternatively, a simple relationship of survival or fertility with population density could be assumed. All in all this would mean between 5 to 10 parameters for the calibration process. Different age classes would be modelled in order to apply age specific culling strategies, but the parameters

of the population dynamics model would apply on the level of the three categories stags, hinds and calves. Standard Kalman filter methodology could be applied for updating and parameter estimation (Harvey, 1989). Furthermore, the dimensionality problem with the current parameter space (16 parameters) would be reduced.

The possible gain achieved by applying the updating algorithm was shown for the example of red deer on Islay. The management model was also used to look at the effects of alternative culling strategies for the Northern Deer Management Groups. However, the practical usefulness of the management model will not be confirmed by theoretical studies but by its use for everyday red deer management in Scotland.

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